Alma Mater Studiorum – Università di Bologna

DOTTORATO DI RICERCA IN

BIODIVERSITA' ED EVOLUZIONE

Ciclo XXII

Settore scientifico-disciplinare di afferenza: BIO 05

TITOLO TESI

INFLUENCE OF ENVIRONMENTAL PARAMETERS ON POPULATION DYNAMICS IN SOLITARY CORALS FROM THE MEDITERRANEAN SEA

Presentata da: Dott. Erik Caroselli

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"With every breath
And all the choices that we make
We are only passing through on her way"

From 'Mother Earth' by Within Temptation

Index

Keywords

Age structure, calcification, computerized tomography, coral growth, demography, Dendrophylliidae, environmental parameters, global warming, growth model, growth rate, latitudinal gradient, linear extension, Mediterranean Sea, population ecology, population stability, reef management, sea surface temperature, skeletal density, solar radiation, solitary coral.

Foreword

Corals have a great ecological, structural, social, economic and long-term monitoring importance (Moberg & Folke 1999). Corals are a fundamental component of marine ecosystems because they: a) channel the energy available at the surface and in the water column to the seabed, b) increase habitat three-dimensional complexity, c) favor the settlement of many organisms that find shelter in the structures they biomineralize, thus increasing biodiversity (Moberg & Folke 1999). Corals and coral reefs - the rain forests of the sea - are the most biodiverse marine ecosystems in the planet (Hoegh-Guldberg et al. 2004). Most corals are symbiotic with unicellular dinoflagellate algae (zooxanthellae), which, due to photosynthesis, provide the host with up to 95% of its necessary energy resources, allowing it to monopolize oligotrophic coastal waters, and introducing further energy into the reef food web (Falkowsky et al. 1984; Muscatine et al. 1984; Bachar et al. 2007). Tropical corals are responsible for the formation of islands and atolls inhabited by thousands of people, and barrier reefs that protect the coasts from erosion, sea waves and tsunamis (Goffredo et al. 2007b). Temperate corals form great superficial waters bioherms and imposing deepwater reefs (Fosså et al. 2002; Kružić & Požar-Domac 2003). Corals and coral reefs provide services to humanity (i.e., bioactive compounds and food resources) and sustain one of the most important economic forces: tourism (Moberg & Folke 1999). Coral skeleton is also a valuable ocean recorder of the environmental conditions in time of accretion: it can give indications about paleoclimate over eons ago, as well as document current detrimental processes, and conversely, provide an important record of recovery events (Cobb et al. 2003).

Most studies on the biology and ecology on the main calcifying group of corals, the order Scleractinia, have been performed in tropical regions, where many species are widely present and can be easily sampled during scientific dives (Freiwald et al. 2004). In the last years rising concern have been expressed by the scientific community about the adverse influence that human activities and climate change (seawater warming and acidification) could have on coral populations, coupled with the cascading effects across foodwebs and with the economic and social repercussions (Solomons et al. 2007).

Coral research in regions outside the range of development of tropical coral reefs (between 30° of latitude north and south) have deserved much less attention, probably because of higher difficulty in collecting the study material (Freiwald et al. 2004), and the Mediterranean Sea is no exception. In the last 10 years, however, there has been growing interest in studying temperate-subtropical species such as Mediterranean corals. The effects of global warming and ocean acidification are expected to be greater in temperate regions and enclosed seas, rather than at the tropics (Solomons et al. 2007), and assessing their effect on Mediterranean marine biodiversity has

been declared an urgent issue by scientists and policymakers of the United Nations (UNEP 2008). Recently, the research group I'm working in (the Marine Science Group, www.marinesciencegroup.org) received a grant from the European Research Council within the "IDEAS Advanced Grant" scheme of the 7th Framework Program of the European Union, for the project "Corals and Global Warming: The Mediterranean versus the Red Sea" (CoralWarm; www.coralwarm.eu), to asses the effects of global warming on Mediterranean and Red Sea corals.

This present study is the first to describe the growth and demographic characteristics in populations of two Mediterranean coral species across a wide latitudinal gradient, and to check for effects of the environmental parameters on their growth and population dynamics.

Chapter I

Variation in biometry and population density of solitary corals with solar radiation and sea surface temperature in the Mediterranean Sea

Abstract

The correlation between two environmental factors (solar radiation and sea surface temperature), biometry and population density was assessed along a latitudinal gradient in the zooxanthellate coral *Balanophyllia europaea*, and in the azooxanthellate coral *Leptopsammia pruvoti*. With increasing polyp size, the oral disc of *B. europaea* assumed an oval shape, while that of *L. pruvoti* retained a circular shape. In both species, biometric parameters varied more with temperature than with solar radiation. In the zooxanthellate species, temperature explained a higher percentage of biometric parameter variance than in the azooxanthellate species. While environmental factors did not co-vary with demographic characteristics in *L. pruvoti*, temperature was negatively related to the population density of *B. europaea.* It is hypothesized that the negative effect of temperature on biometry and population density of *B. europaea* depends on photosynthesis inhibition of symbiotic zooxanthellae at high temperatures, which would lower the calcification rate and energetic resources availability.

Introduction

The variation of environmental parameters due to latitude is a substantial causal factor of the global distribution of corals (Kleypas et al. 1999). The distribution of atolls and main coral reefs of the world, confined between 30° N and 30° S latitude (Kinsey & Davies 1979), suggests that coral growth actually decreases at high latitudes to a point where coral reef development no longer occurs (Grigg 1982). Coral "growth" is a composite of the three related characters of annual calcification, skeletal density and linear extension rate (calcification = skeletal density x linear extension; Lough & Barnes 2000; Carricart-Ganivet 2004), and their measurement is essential when assessing effects of environmental parameters on coral growth (Dodge & Brass 1984). These three variables have been studied along a latitudinal gradient in the genera *Porites* (Grigg 1982; Lough & Barnes 2000) and *Montastraea* (Carricart-Ganivet 2004) and variation in the three parameters has been related to variation in temperature and light associated with latitude. In colonies of the genus *Porites* in the Hawaiian archipelago, Australian Great Barrier Reef, and Thailand, negative correlations with latitude were found for the linear extension, leading to an increase in skeletal density of the colonies (Grigg 1982; Lough & Barnes 2000). In colonies of the genus *Montastraea* in the Gulf of Mexico and Caribbean Sea, negative correlations with latitude were found for calcification and skeletal density, leading to an increase in linear extension rate (Carricart-Ganivet 2004). Rates of linear extension in colonial corals of the genera *Pocillopora* and *Acropora* and in a number of species of the Faviidae family in subtropical Australia (Crossland 1981; Stimson 1996; Harriott 1999) were considerably slower than those at low latitude. Also in solitary corals of the Fungiidae family a negative relationship was found between growth rate and latitude (Goffredo & Chadwick-Furman 2003). In contrast, there seem to be cases where rates of coral growth do not vary with increasing latitude. For instance, *Acropora yongei*, *Acropora formosa*, *Turbinaria frondens* and *Porites heronensis* from subtropical Australia have linear extension rates similar to those of closely related taxa in the tropics, confounding any causal link between latitude, growth rates of coral colonies or coral reefs (Harriott 1999).

For temperate areas, studies on the relationship between environmental parameters and coral growth are scarce. In *Astrangia danae* (Jacques et al. 1983) and *Plesiastrea versipora* (Howe & Marshall 2002), calcification rate increases with temperature, similar to the trend in tropical corals, albeit at lower temperatures. This study presents the relationship between latitudinal variation of environmental factors (solar radiation and sea surface temperature) and biometry and population density of two Mediterranean Sea corals, *Balanophyllia europaea* (Risso, 1826) and *Leptopsammia pruvoti* Lacaze-Duthiers, 1897.

B. europaea is a solitary, ahermatypic, zooxanthellate, scleractinian coral, which is endemic to the Mediterranean Sea (Zibrowius 1980). Due to its symbiosis with zooxanthellae, the distribution of this coral is restricted to 0-50 m depth (Zibrowius 1980), where its population density can reach dozens of individuals per square meter (Goffredo et al. 2004a). Its reproductive biology is characterized by simultaneous hermaphroditism and brooding (Goffredo et al. 2002). *L. pruvoti* is an ahermatypic, azooxanthellate, solitary, scleractinian coral, which is distributed in the Mediterranean basin and along the European Atlantic coast from Portugal to southern England. It is one of the most common organisms under overhangs, in caverns, and crevices at 0-70 m depth, reaching densities of thousands of individuals per square meter (Zibrowius 1980; Goffredo et al. 2006). Its reproductive biology is characterized by gonochorism and brooding (Goffredo et al. 2006).

The aim of this study is to assess the variation in the biometric parameters and population density of the zooxanthellate *B. europaea* and of the azooxanthellate *L. pruvoti* along a solar radiation and sea surface temperature gradient.

Materials and methods

From 9th November 2003 to 30th September 2005, specimens of *Balanophyllia europaea* and *Leptopsammia pruvoti* were collected from six sites along a latitudinal gradient, from 44° 20' N to 36° 45' N (Figure 1). Latitude is the main factor influencing the variation of temperature and light (Kain 1989), which are the two environmental parameters considered in this study since they are strongly linked to coral biometry, physiology and demography (Kleypas et al. 1999; Lough & Barnes 2000; Harriott & Banks 2002; Al-Horani 2005). At each site, a transect was sampled for both species. For *B. europaea* the transect consisted of 3 patches of 1 m^2 each, arranged in a line, 5 m apart and situated along a reef exposed south at a depth of 5-7 m. For *L. pruvoti* the transect consisted of at least 3 patches of 0.00425 m^2 each, situated on the vault of crevices 3 m apart, at a depth of 15-17 m (Site and number of patches for *B. europaea*: Genova n = 8, Calafuria n = 18, Elba n = 3, Palinuro n = 3, Scilla n = 8, Pantelleria n = 3; site and number of patches for *L. pruvoti*: Genova n = 3, Calafuria n = 3, Elba n = 4, Palinuro n = 3, Scilla n = 3, Pantelleria n = 3). Regular spacing of quadrats and transects may be biased if laid over a population with a natural regular spacing. However, this should not have occurred in these cases since the distributional pattern of the two species is disaggregated (random) (personal observation; Goffredo & Zaccanti 2004; Goffredo et al. 2004a). All of the coral polyps present were collected from each patch. The sampling was performed at depths known to have high population densities and where the reproductive biology of the two species had been studied previously (Goffredo & Zaccanti 2004; Goffredo et al. 2002,

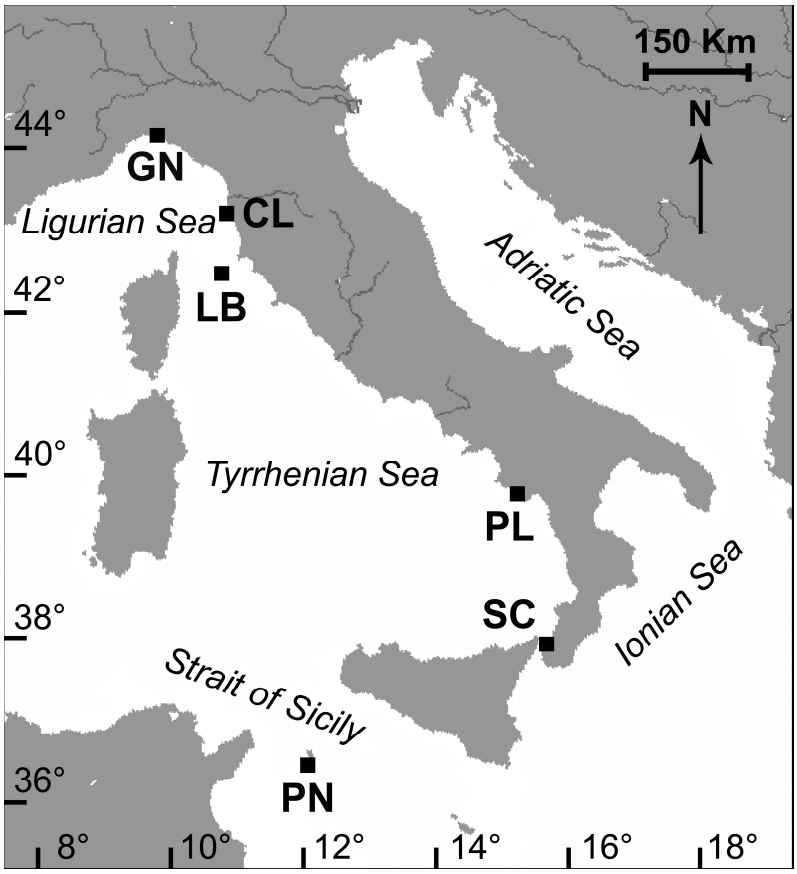

Fig. 1 Map of the Italian coastline indicating sites where corals were collected. Abbreviations and coordinates of the sites in decreasing order of latitude: GN Genova, 44°20'N, 9°08'E; CL Calafuria, 43°27'N, 10°21'E; LB Elba Isle, 42°45'N, 10°24'E; PL Palinuro, 40°02'N, 15°16'E; SC Scilla, 38°01'N, 15°38'E; PN Pantelleria Isle, 36°45'N, 11°57'E.

2004a, 2006). The area of each patch was smaller for *L. pruvoti* than for *B. europaea* because of the very high density of the former species, and the difficulty of sampling on the vaults, inside narrow caves.

Collected corals were dried at 50 °C for four days, then observed under a binocular microscope to remove fragments of substratum and calcareous deposits produced by other organisms. A low drying temperature was chosen to avoid phase transitions in the skeletal aragonite/calcite composition (Vongsavat et al. 2006), as this problematic will be investigated using these samples in a diffractometric analysis in preparation. Polyp length (*L*: maximum axis of the oral disc), width (*W*: minimum axis of the oral disc) and height (*h*: oral-aboral axis) were measured using a pair of calipers and dry skeletal mass (*M*) was measured using a precision balance (Goffredo & Chadwick-Furman 2003; Goffredo et al. 2002). Polyp volume (*V*) was determined by applying the formula $V = \frac{L}{2} \times \frac{W}{2} \times h\pi$ (Goffredo et al. 2002, 2006). Skeletal density (*D*) was calculated by dividing *M* by *V*. The population density was obtained as: (1) *NI*, number of individuals per area unit (N m^{-2}), (2) *G*, grams per unit area (g m^{-2}), (3) *P*, percent coverage.

All data relating to the Calafuria site of *B. europaea* were taken from the dataset of Goffredo et al. (2004a), where the biometric analysis was performed on 75 polyps collected randomly at 6 m, and several patches were sampled between 0-13 m to examine the bathymetric distribution. For the biometric analysis the same 75 polyps were used in this work, while for the correlation analysis

between biometry, population density and environmental parameters, only the patches sampled between 5-7 m were considered.

As done by a number of authors (e.g. Harriott 1999; Lough & Barnes 2000; Carricart-Ganivet 2004; Peirano et al. 2005a, b) in their studies on the influence of environmental parameters on coral growth, also in this study physical measurement data (Sea surface temperature and solar radiation) have been obtained from data banks. During 2003-2005, sea surface temperature (SST) data were obtained for each site from the National Mareographic Network of the Agency for the Protection of the Environment and Technical Services (APAT, available at http://www.apat.gov.it). These data are measured by mareographic stations SM3810, manufactured by the Italian Society for Precision Apparatuses (SIAP), placed close to the sampling sites. Mean annual SST was obtained from hourly values measured from January 2001 through January 2005 (number of hourly values = 35,064 for each site). Monthly values of solar radiation (W m^{-2}) were obtained from the International Cloud Climatology Project (ISCCP; available at http://ingrid.ldgo.columbia.edu/). These estimates are derived from satellite measurements of cloud and atmospheric optical properties. Mean annual solar radiation of each site was obtained for the 2.5°-latitude-by-longitude square associated with each of the 6 sites (number of monthly values = 48 for each site).

Statistical analyses

Spearman's rank correlation coefficient is an alternative to Pearson's correlation coefficient (Altman 1991). It is useful when data are non-normally distributed, and thus the assumptions of Pearson's correlation coefficient are not met. Spearman's rank correlation coefficient was used to calculate the significance of the correlations between biometric parameters and environmental variables, and between population density and environmental variables.

Kruskal-Wallis test is a non parametric alternative to the analysis of variance (ANOVA), and is used to compare groups of means. The advantage of this test is that the assumption of normality of data is not required, as the test is based on the ranks of data. This distribution-free test proved to be more robust than its parametric counterpart in the case of non-normal distribution of sample data, and is a viable alternative to parametric statistics (Potvin & Roff 1993). Kruskal-Wallis test was used to compare mean solar radiation, SST, polyp length and population density among study sites.

Covariance analysis (ANCOVA) is a combination of linear regression and variance analysis (Altman 1991). It can be used to compare the regression equations between different groups. For example, given the linear regression equations between the same two variables of three groups of treatments, the analysis compares the slopes and intercepts of the three equations. ANCOVA was

used to compare the relationships between biometric parameters and polyp length among patches and among study sites.

Monte Carlo method (Gabriel & Lachenbruch 1969) solve problems in non parametric test for small samples. In fact it estimates the p-value by taking a random sample from the reference set and studies its permutations (Senchaudhuri et al. 1995). My Monte Carlo estimate for p used 100,000 random permutations. This method was used to estimate the significance of the Kruskal-Wallis test when comparing the mean population densities among study sites for both species.

Kruskal-Wallis tests, Spearman's correlation coefficients, and Monte Carlo corrections for small sample size were calculated with SPSS 12.0 (Apache Computer Software Foundation).

Results

Solar radiation and SST both varied among the sites (Kruskal-Wallis test, degrees of freedom = 5, $p < 0.001$; Figure 1). While solar radiation correlated negatively with latitude, SST correlated significantly after exclusion of Genova-Portofino (GN) site from analysis (Fig. 2). The GN site is characterized by particular local conditions (xeroterm site because of local currents and rock composition; APAT, available at http://www.apat.gov.it) and typically has higher SSTs than expected at that latitude (annual SST of Ligurian Sea = 18 °C, Genova-Portofino (GN) = 19.6 °C); (Figure 1).

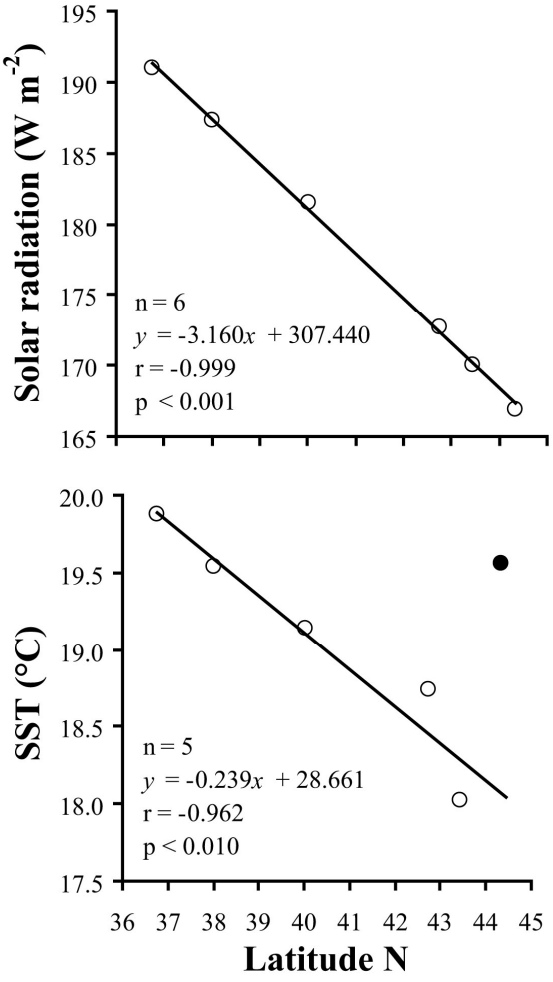

Fig. 2 Relationship between environmental parameters (mean annual solar radiation and SST) and the latitude of study sites along the coast of Italy. The black dot indicates the site of Genova-Portofino, which was characterized by special local conditions that cause a temperature deviation from the norm at that latitude, and thus was excluded from the correlation coefficient calculation. n = number of stations; r = Pearson correlation coefficient.

Polyp length (Figure 3) was selected as the main biometric parameter since it is a good indicator of skeletal mass and has been used as the measure of size in biometric, reproductive biology, and population dynamic studies of *Balanophyllia europaea*, *Leptopsammia pruvoti,* and other solitary corals (Hoeksema 1991; Bell & Turner 2000; Goffredo & Chadwick-Furman 2003; Goffredo et al. 2002, 2004a, 2006). Polyp width, height, volume, and skeletal mass all correlated positively with polyp length in both coral species examined (Figures 4 and 5). Skeletal density correlated positively with polyp length in *B. europaea* at only two sites (Palinuro and Pantelleria). In contrast, skeletal density correlated negatively with polyp length in *L. pruvoti* at all sites (Figures 4 and 5). In both coral species, the relationships between biometric parameters and polyp length varied significantly among the study sites (covariance analysis, degrees of freedom between exponents = 5; $p < 0.05$). Each relationship between the biometric parameters and polyp length was linearized and the obtained slopes (representing the original equation exponent) were compared among study sites. None of the slopes was homogeneous among study sites.

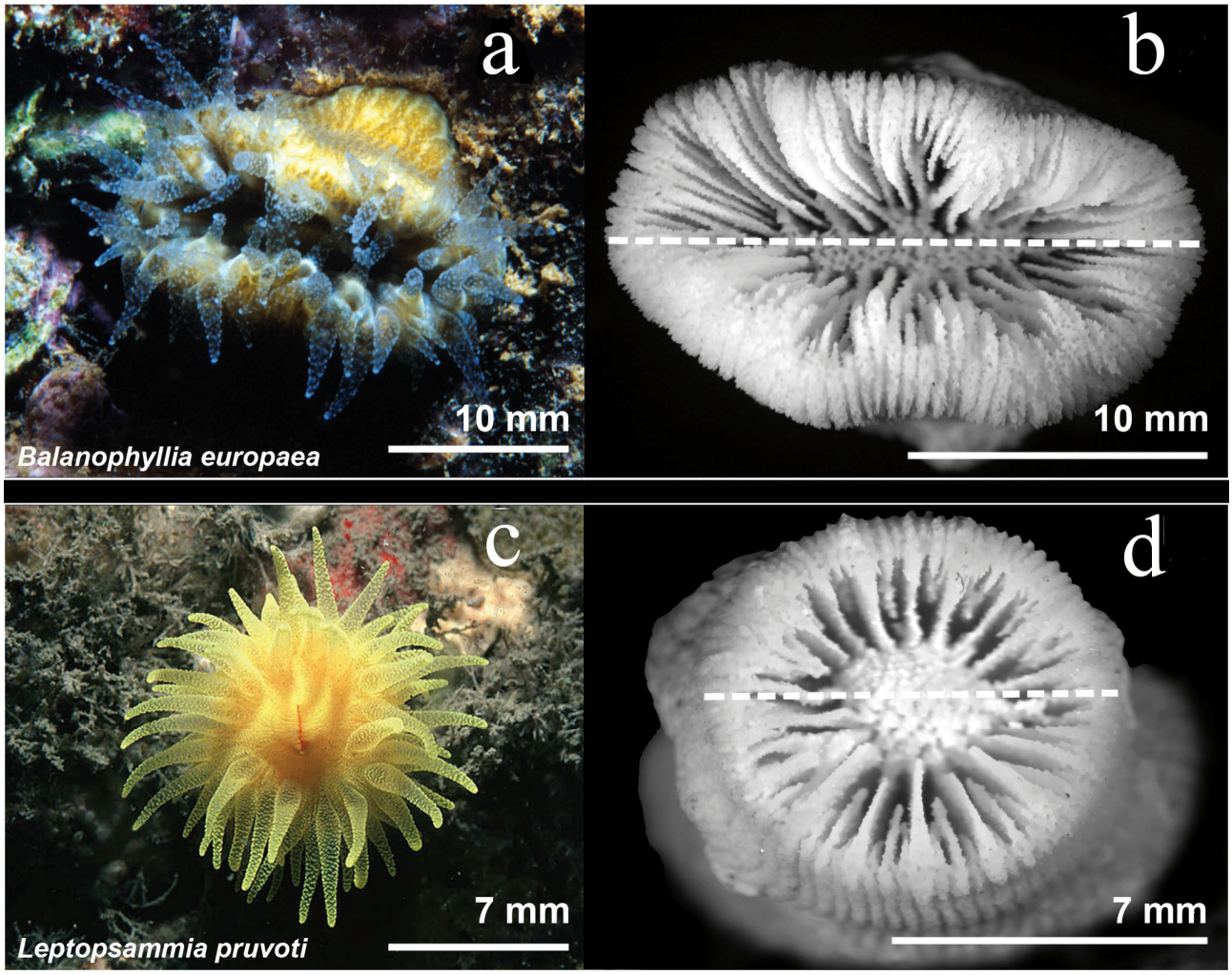

Fig. 3 *Balanophyllia europaea* (a living polyp**;** b corallite) and *Leptopsammia pruvoti* (c living polyp**;** d corallite) specimens from Genova-Portofino. Dotted line indicates polyp length (*L*: maximum axis of the oral disc).

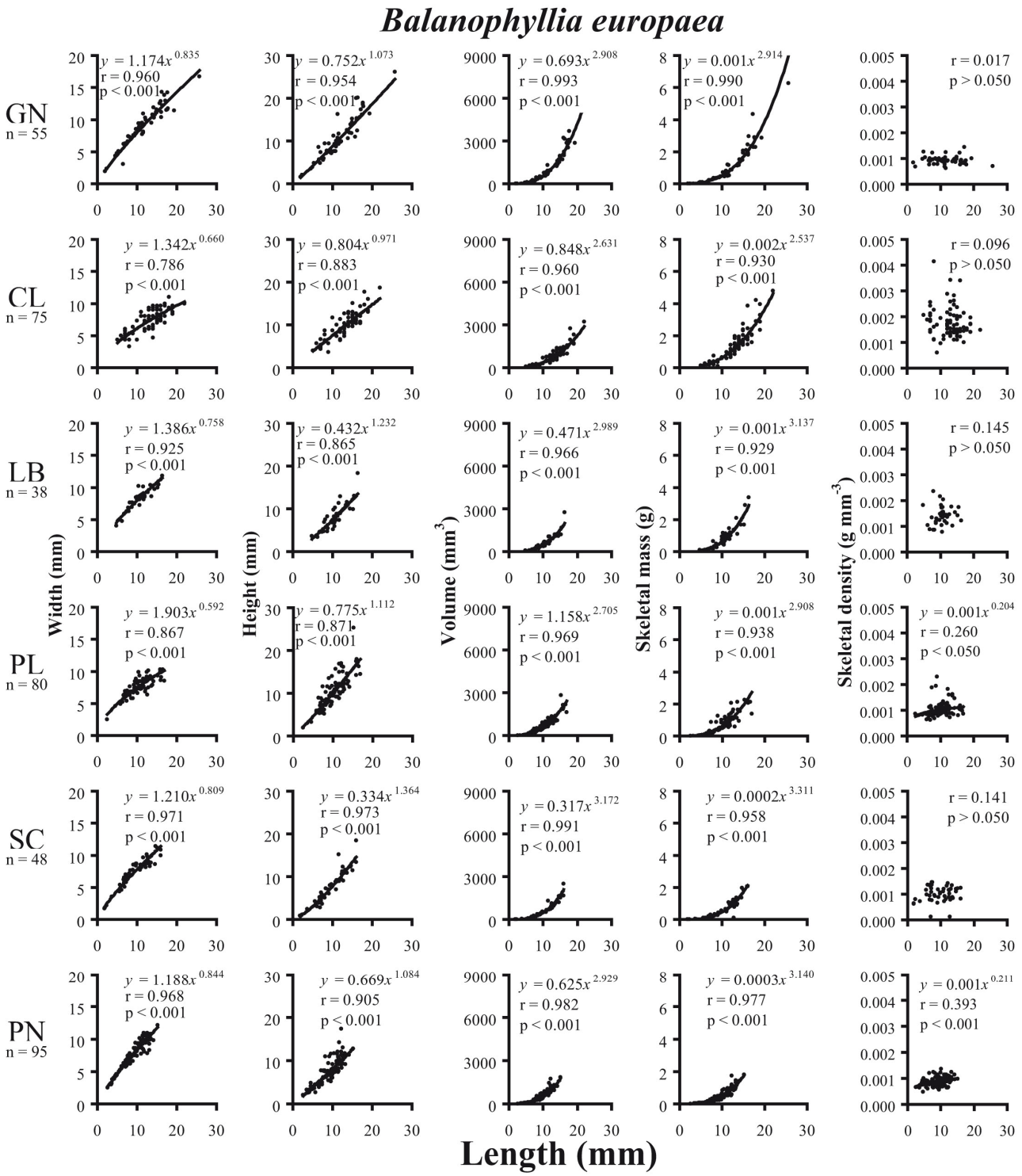

Fig. 4 *Balanophyllia europaea*. Dependence of biometric parameters on polyp length at six sites along the western coast of Italy (GN Genova-Portofino, CL Calafuria, LB Elba, PL Palinuro, SC Scilla, PN Pantelleria). n = number of individuals; r = Pearson correlation coefficient. The sites are arranged in order of decreasing latitude.

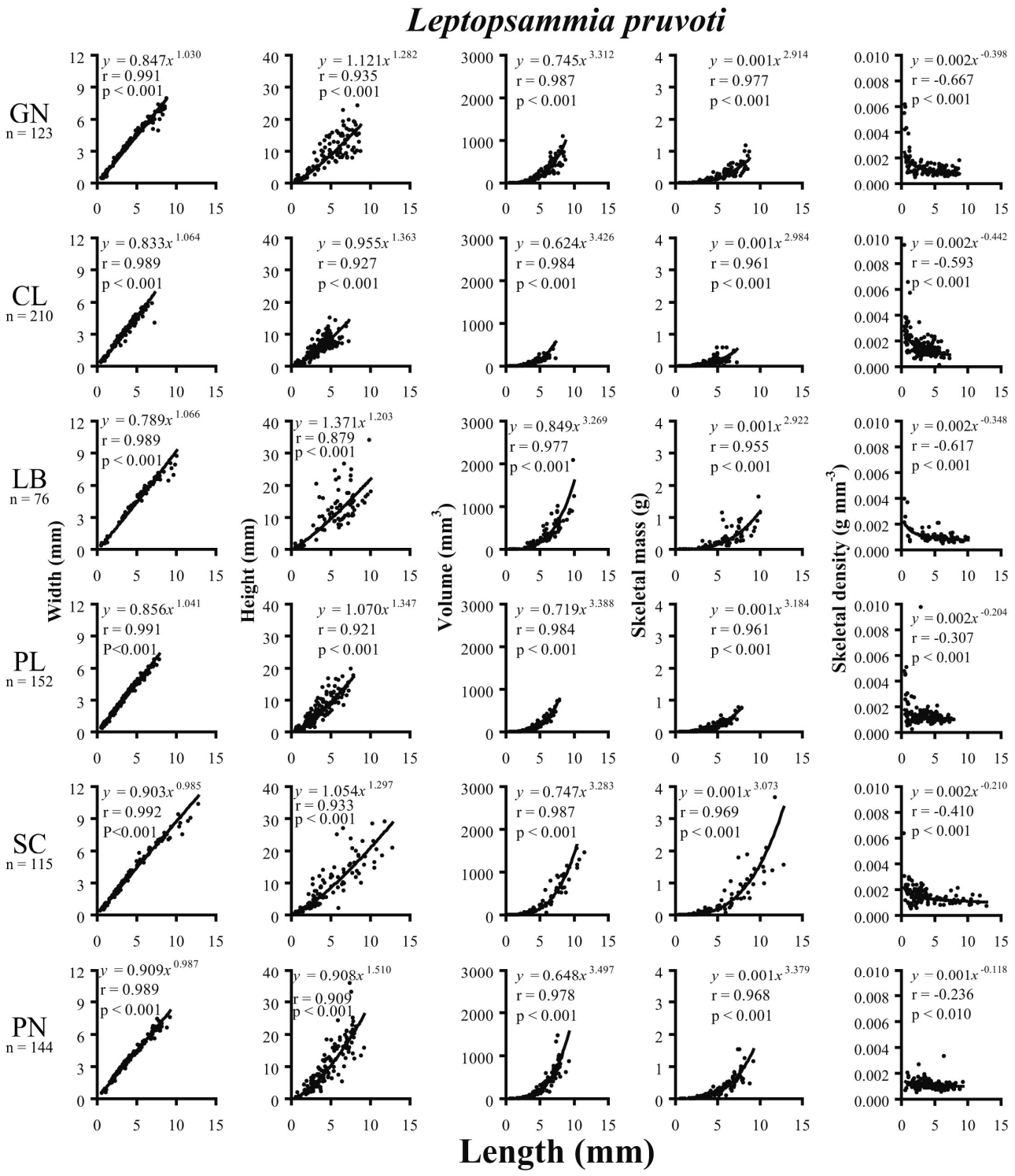

Fig. 5 *Leptopsammia pruvoti*. Dependence of biometric parameters on polyp length at six sites along the western coast of Italy (GN Genova-Portofino, CL Calafuria, LB Elba, PL Palinuro, SC Scilla, PN Pantelleria). n = number of individuals; r = Pearson correlation coefficient. The sites are arranged in order of decreasing latitude.

The increase in polyp width in comparison with that of polyp length differed in the two species (Figures 4 and 5). In *B. europaea,* an allometric relationship was found; length increased more rapidly than did width, which resulted in an oval oral disc as polyp size increased (at all sites, the confidence interval CI of the regression equation exponent was < 1, 0.52-0.90, CI 95%, degrees of freedom = 37-94, Figure 4). *L. pruvoti* had either isometric growth (at Scilla and Pantelleria, the confidence interval of the regression equation exponent contained 1, 0.96-1.01, CI 95%, degrees of freedom = 114-143) or allometric growth, with polyp length increasing less quickly than did width (at Genova-Portofino, Calafuria, Elba and Pantelleria, the confidence interval of the regression equation exponent > 1, 1.00-1.10, CI 95%, degrees of freedom = 75-209, Figure 5) which resulted in a circular oral disc as polyp size increased.

In both species, the lengths of sampled individuals differed significantly among the sites (Kruskal-Wallis test, degrees of freedom = 5, $p < 0.001$). For this reason, analyses of correlations between environmental variables and biometric parameters were performed after applying to the data the method of the adjusted values in relation to length (Steel 1980). In *B. europaea,* whereas polyp length, width, height and volume positively correlated with solar radiation and SST, skeletal mass and skeletal density were negatively correlated (Figure 6). In all cases, SST explained 2.5 to 7.4 times more of the variance than did solar radiation (the percentage of biometric parameter variance explained by SST ranged from 3.9% for length to 63.8% for skeletal mass; Figure 6). In *L. pruvoti*, solar radiation did not correlate with any biometric parameter. Polyp length, height, volume and skeletal density were correlated with SST, which explained from 0.5% of the variance for volume to 1.2% for length (Figure 6). SST was more highly correlated with biometric parameters in *B. europaea* than in *L. pruvoti* (r^2 of the relationship between biometric parameters and SST was 3 times higher for length to 638 times higher for skeletal mass).

In *B. europaea*, population density varied significantly among the sites (Kruskal-Wallis test, Monte Carlo correction for small sample size, degrees of freedom = 5, $p < 0.001$), and was negatively correlated with SST (Figure 7). In *L. pruvoti*, population density did not vary among the sites (Kruskal-Wallis test, Monte Carlo correction for small sample size, degrees of freedom = 5, $p > 0.05$). Mean population density for *L. pruvoti* was 10.155 individuals m^{-2} (SE = 1.317), 2030 grams m^{-2} (SE = 232), and 15.4 percent cover (SE = 1.4).

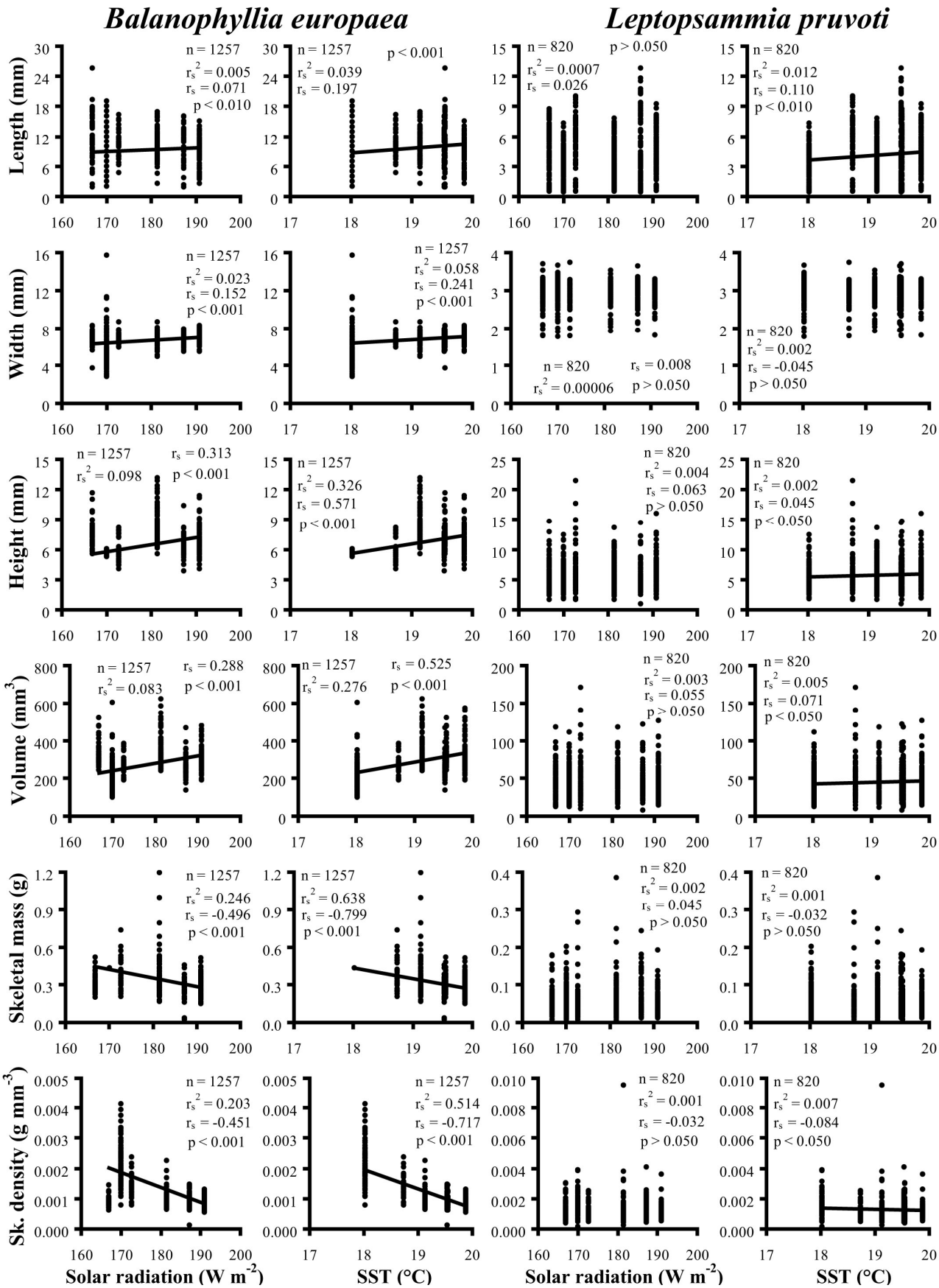

Fig. 6 Variation in the biometric parameters of two corals, *Balanophyllia europaea* and *Leptopsammia pruvoti* with environmental variables (annual mean solar radiation and SST). r_s^2 = Spearman's determination coefficient; n = number of individuals. Note that scale of the ordinate axes differs between the species.

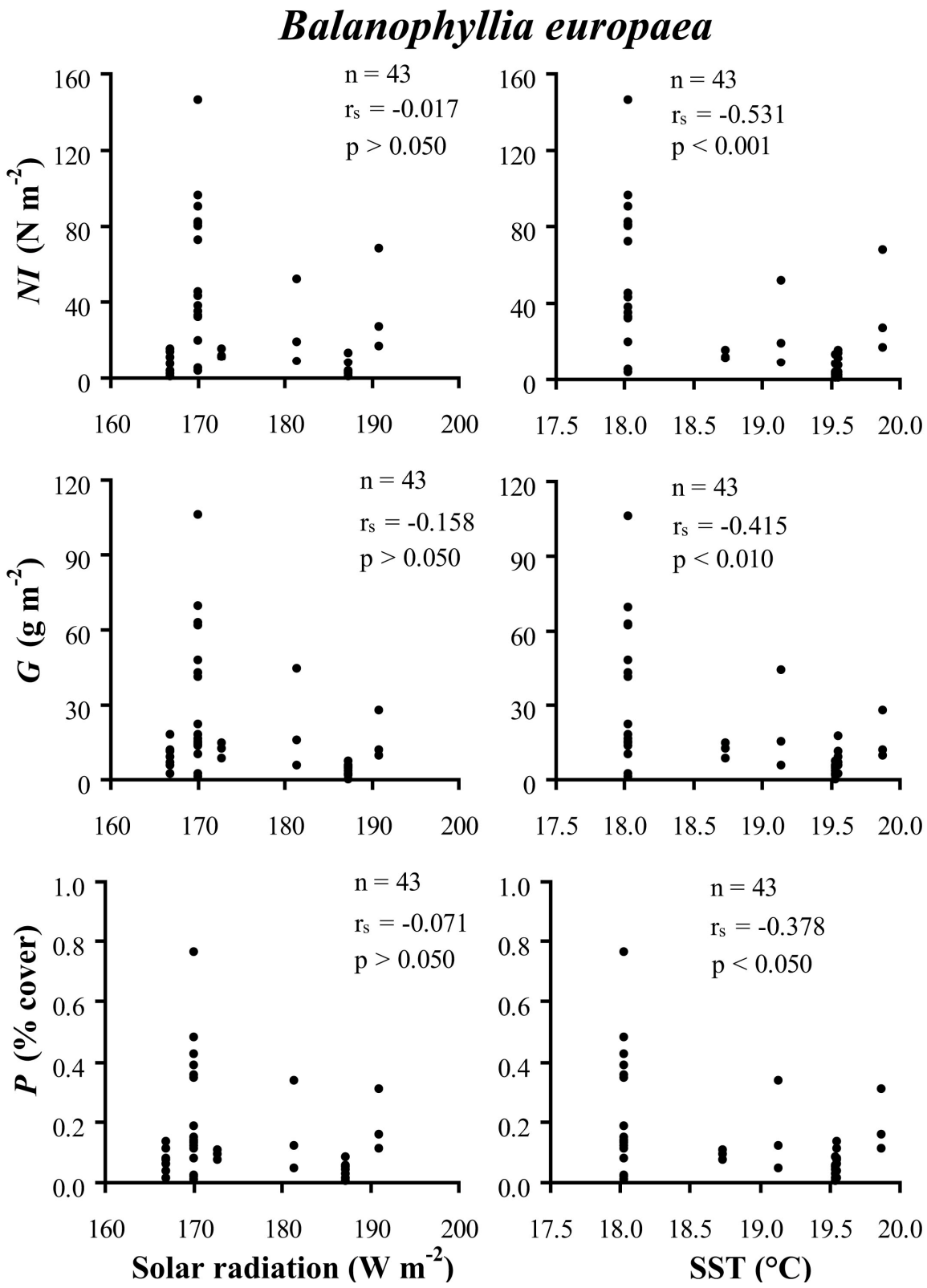

Fig. 7 *Balanophyllia europaea*. Variation in population density parameters with environmental variables (mean annual solar radiation and SST). *NI* = number of individuals per square meter, *G* = grams per square meter, *P* = percent cover. r_s = Spearman's correlation coefficient; n = number of quadrats examined. Correlations for *Leptopsammia pruvoti* are not shown because population density was homogeneous among the sites examined.

Discussion

The difference between the two species in the relationship between skeletal density and polyp size can be interpreted in terms of relationship between calcification and linear extension. As polyp size of *Balanophyllia europaea* increases, there is a progressive decrease in linear extension rate (Goffredo et al. 2004a). A parallel diminution of the calcification rate could explain the maintenance of skeletal density among mean values of 0.001-0.002 g mm^{-3} regardless of polyp size, at 4 of the 6 sites studied (Genova-Portofino, Calafuria, Elba, Scilla). At the Palinuro and Pantelleria sites, calcification rate could decrease less quickly than did linear extension rate, causing a positive correlation between skeletal density and polyp size. In *Leptopsammia pruvoti*, as known for several other solitary corals (Bablet 1985; Yamashiro & Nishihira 1998; Goffredo & Chadwick-Furman 2003; Goffredo et al. 2004a), the linear extension rate should decrease with increasing polyp size. The diminution of skeletal density with increasing polyp size may have been due to a greater decrease in calcification than in linear extension rate. The radiological analyses underway on both species are expected to provide an understanding of the relationship between calcification and linear extension rates.

The difference in the biometric relationship between the oral disc axes between the two species may relate to sedimentation stress. Sedimentation has many negative effects on corals, including prevention of growth and calcification, interference with respiration, nourishment and photosynthesis, increase in energy dissipation, damaging polyp tissues, lowering the fecundity and interfering with substratum colonization process (Rosenfeld et al. 1999, and references therein). Corals can adopt different strategies to prevent these negative effects, i.e., sediment rejection behavior or resistant growth forms (Stafford-Smith & Ormond 1992; Bell & Turner 2000). The oval form of the oral disc is one of these resistant forms, since it decreases the area affected by sedimentation and favors the removal of sediment from the polyp surface (Hoeksema 1991). The allometric relationship between polyp width and length in *B. europaea*, which produces a progressively oval-shaped oral disc, may prevent damage from sedimentation that might otherwise occur as the polyp becomes larger (Goffredo et al. 2004a). In corals living on vertical walls, the removal of sediment is carried out by gravity, rather than by active mechanisms (Stafford-Smith & Ormond 1992). Moreover, in shallow waters overhangs of the Ligurian Sea, a thin coat of sediment covers the vertical surfaces, while it is absent on down-facing surfaces (Virgilio et al. 2006). *L. pruvoti* polyps, characterized by circular oral discs, do not need growth forms resistant to damage from sedimentation, since they colonize the vaults of caves and crevices with their oral pole directed downwards.

The SST environmental variable correlated with biometric parameters more strongly than did solar radiation in both species. This relationship is more marked in *B. europaea*, which is zooxanthellate, suggesting a possible effect of temperature on photosynthesis in the algal symbionts. In zooxanthellate corals, photosynthesis enhances calcification (Gattuso et al. 1999; Al-Horani et al. 2005), and both processes have temperature optima (Howe & Marshall 2002; Al-Horani 2005). In *B. europaea,* the decrease in skeletal density with increasing SST could depend on an attenuation of calcification due to an inhibition of the photosynthetic process at higher temperatures. In *L. pruvoti*, the weak relationship between temperature and skeletal density could be due to the absence of zooxanthellae, and thus lack of a physiological dependence of calcification on photosynthesis.

The spatial distribution of adult corals is influenced by the number of offspring produced per reproductive event and their dispersal capability (Hughes et al. 2000). Theoretically, low fecundity combined with wide larval dispersal results in a low density of local populations. In contrast, high fecundity combined with limited larval dispersal produces high local population density (Gerrodette 1981; Carlon 2002; Goffredo & Zaccanti 2004; Goffredo et al. 2004a). In symbiotic corals, a large portion of the energy needed for gametogenesis and larval development is supplied by photosynthate from the zooxanthellae (Rinkevich 1989). The low population density of *B. europaea* relative to that of *L. pruvoti* could be due to lower polyp fecundity and the greater dispersion capability of its larvae (Goffredo & Zaccanti 2004; Goffredo et al. 2002, 2004a, 2006). However, population density also depends on recruitment and mortality due to various factors, including predation, so this hypothesis requires further testing. The decrease in population density of *B. europaea* with increasing SST might depend on a polyp's reduced fecundity, consequent to a decrement of the photosynthetic efficiency of the symbiont zooxanthellae at higher than optimal temperatures (Al-Horani 2005), resulting in lower energy resources for gametogenesis (Rinkevich 1989; Carlon 2002). Without utilizing photosynthesis, *L. pruvoti* would maintain its population density around the mean value regardless of the SST. Further studies on the reproductive biology of these two species at different sites situated along a latitudinal gradient might clarify the relationship between polyp fecundity and SST.

In conclusion, it is hypothesized that the high temperature is a negative factor for the zooxanthellate *B. europaea*, since it would lower the photosynthetic efficiency of its symbionts, causing negative effects on both polyp growth and colonization process, while it would not significantly influence the azooxanthellate *L. pruvoti*. An alternative explanation for the decrease of skeletal and population density of *B. europaea* with increasing temperature could be related to suspension feeding. In the Mediterranean Sea, nutrient levels and zooplankton availability are

typically lower in summer-fall (i.e. high temperature) than in winter-spring (i.e. low temperature; Coma et al. 2000; Coma & Ribes 2003). Low nutrients and zooplankton availability cause stress and starvation in *Cladocora caespitosa* (Peirano et al. 2005a), and a summer dormancy in the metabolism of several benthic suspension feeding taxa (Coma et al. 2000, Coma & Ribes 2003). Moreover, in *Stylophora pistillata* colonies, starved corals present significantly lower levels of calcification and photosynthesis than fed corals (Houlbrèque et al. 2004). Low energetic resources could be the causes of low skeletal and population density in *B. europaea* at high temperatures. However, if this was the case, the inhibition would be supposed to be stronger in *L. pruvoti*, which is a full heterotrophic, than in *B. europaea*, which can rely on the symbiont. In contrast, we found that skeletal and population density of *L. pruvoti* are almost the same in low and high temperature study sites, thus the hypothesis of a photosynthetic inhibition at high temperatures seems to be more appropriate. Anyways, other factors such as pollution could influence the spatial distributions of populations. During the sampling period of this study, the Italian Ministry of the Environment and Land and Sea Protection conducted sea water quality surveys along the Italian coasts, based on basic oceanographic data (NO_3^-, NO_2^-, NH_4^+, PO_4^{3-}, SiO_4^{4-}, salinity, chlorophyll and transparency, which are parameters included in the Sea Water Classification; Seawater Monitoring Program, available at www2.minambiente.it/sito/settori_azione/sdm/pubblicazioni/pubblicazioni.asp; www.sidimar.ipzs.it). Ministry data exhibited negative correlations between latitude and environmental quality along the western coasts of Italy, but this is hardly linkable to my data since I found that the population density of both species does not co-vary with latitude.

Future work to test the hypothesis of an inhibition of photosynthetic efficiency of *B. europaea* at high temperatures will involve experimental measurements of photosynthesis at different temperatures and stable isotopes analyses on *B. europaea* skeletons to reconstruct the photosynthetic efficiency of the polyps.

Chapter II

Relationships between growth, population structure and sea surface temperature in the temperate solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae)

Abstract

The demographic characteristics of the solitary zooxanthellate scleractinian *Balanophyllia europaea*, endemic to the Mediterranean, were determined in six populations, on a latitudinal gradient along the Italian coast, and compared with the mean annual sea surface temperature (SST). Growth rate correlated negatively, and asymptotic length of the individuals positively with SST. With increasing SST, the distributions of age frequencies moved away from a typical steady state structure (i.e., exponential decrease in the frequency of individuals with age), indicating less stable populations and showed a deficiency of individuals in the younger-age classes. These observations suggest that high temperatures are an adverse factor to the *B. europaea* symbiosis. Using projected increases in seawater temperature, most of the *B. europaea* populations in the Mediterranean are expected to be close to their thermal limits by 2100 and the populations at that time may support few young individuals.

Introduction

Latitude differences in temperature and irradiance are an important influence on global coral distribution patterns (Kleypas et al. 1999). In general, coral growth decreases with increasing latitude, to a point beyond 30°N and 30°S where coral-reef development no longer occurs (Kinsey & Davies 1979; Grigg 1982). For temperate regions, studies on the relationship between environmental parameters and coral growth are scarce. For *Astrangia danae* (Jacques et al. 1983) and *Plesiastrea versipora* (Howe & Marshall 2002), calcification rate has been shown to increase with temperature, similar to the trend observed in tropical corals (Lough & Barnes 2000; Carricart-Ganivet 2004; McNeil et al. 2004), but for the zooxanthellate coral *Balanophyllia europaea,* Goffredo et al. (2007a) reported a negative correlation between sea surface temperature (SST) and skeletal and population density.

There is limited information available on population dynamics of scleractinian corals. In 1973 the modest amount of data collected over the previous 30 years was reviewed and parameters such as growth and survivorship were described (Connell 1973). Since then, demographic processes have been described for some species in the Red Sea (Loya 1976; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003; Glassom & Chadwick 2006; Guzner et al. 2007), Northeastern Pacific (Fadlallah 1983), Caribbean (Hughes & Jackson 1985; Johnson 1992; Meesters et al. 2001; Vermeij 2006), Great Barrier Reef (Babcock 1991), and the Mediterranean (Goffredo et al. 2004a; Shenkar et al. 2005). The paucity of information on population dynamics of most scleractinian corals can be attributed, partly, to a distortion of the age-size relationships in this group, resulting from processes of fragmentation, fusion and partial colony mortality (Hughes and Jackson 1985; Babcock 1991; Hughes et al. 1992). These phenomena prevent the application of traditional growth and population dynamic models based on organism age, and create very complex demographic patterns (Hughes & Jackson 1985). However, in species where the individuals rarely fragment or fuse and partial mortality is discernable by anomalies in the regular growth pattern, it is possible to determine coral age (Chadwick-Furman et al. 2000).

Growth band analysis is a technique that can be used to determine the age of certain forms of gorgonian and scleractinian, solitary and colonial corals, and to describe their demographic characteristics by applying age-based growth and population dynamics models (Knuston et al. 1972; Buddemeier et al. 1974; Grigg 1974; Mistri & Ceccherelli 1994; Peirano et al. 1999; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003; Goffredo et al. 2004a; Goffredo & Lasker 2006). Demographic parameters reveal relationships between organisms and their environment, contributing to habitat stability assessment (Grigg 1975; Meesters et al. 2001). The demographic analysis of coral populations can reveal the level of stress to which they are

subjected (Bak & Meesters 1999; Guzner et al. 2007). In addition, information on population turnover aids in the development of techniques for the restoration of damaged or degraded coastal areas (Chadwick-Furman et al. 2000; Epstein et al. 2001; Goffredo & Chadwick-Furman 2003).

B. europaea (Risso, 1826) is a solitary, ahermatypic, zooxanthellate scleractinian coral, which is endemic to the Mediterranean (Zibrowius 1980). Because of its symbiosis with zooxanthellae, it is restricted to depths of 0-50 m (Zibrowius 1980), where the population density can reach dozens of individuals per square meter (Goffredo et al. 2004a). Its reproductive biology is characterized by simultaneous hermaphroditism and brooding (Goffredo et al. 2002). Goffredo et al. (2007a) examined the correlations between SST, biometry and population density of this species and a closely related one, the azooxanthellate *Leptopsammia pruvoti*, along the Italian coasts. They found a negative correlation between mean annual SST and skeletal and population density in *B. europaea*, but no correlation in *L. pruvoti*. To explain these results, they hypothesized that the negative effects on *B. europaea* skeletal and population density could be related to an inhibition of the photosynthesis of *B. europaea* symbiotic zooxanthellae at high temperatures.

This present study aimed to assess growth rates and population structure variation of *B. europaea* along a latitudinal gradient of mean annual SST. Considering the negative effects of temperature on the *B. europaea* symbiosis (Goffredo et al. 2007a), it was expected that the same negative trend, shown by biometry and population density, would also apply to growth and population structure. Consequently, this study tested the hypothesis that high temperature has a negative effect on growth rates and population structure of *B. europaea*.

Materials and methods

Sample collection

From 9th November 2003 to 30th September 2005, specimens of *Balanophyllia europaea* were collected from six populations along a latitudinal gradient, from 44°20'N to 36°45'N (Fig. 1). Latitude is the main factor influencing the variation in SST (Kain 1989), which is the environmental parameter considered in this study because it has been shown to be strongly linked to coral growth, physiology and demography (Kleypas et al. 1999; Lough & Barnes 2000; Al-Horani 2005). With the exception of the Calafuria population, for which data were obtained from a previous study (Goffredo et al. 2004a), samples were collected for each population using transects that consisted of at least 3 patches of 1 m^2 each, arranged in a line 5 m apart along the southern side of each reef at a depth of 5-7 m. Because the distribution pattern of *B. europaea* is random, the problems associated with regularly spaced quadrats and transects do not apply to this study (Goffredo & Zaccanti 2004; Goffredo et al. 2004a). All of the polyps present were collected from each patch. The sampling was

at depths known to have high population densities and where the reproductive biology, biometry, and population density of this species had been studied previously (Goffredo et al. 2002, 2004a, 2007a; Goffredo & Zaccanti 2004). Choosing the sampling depth based on maximum abundance may bias growth toward a higher rate, and in turn underestimate age, but by sampling in the depth range of 5-7 m where 62% of this species are found (Goffredo et al. 2004a) this maximum-abundance bias is reduced.

Sample analysis

Corals were dried at 50°C for four days and observed under a binocular microscope to remove fragments of substratum and calcareous deposits produced by other organisms. Corallite length was selected as the main biometric parameter, since it is a good indicator of skeletal mass and has been used as the primary measure of size in other biometric, reproductive biology and population dynamics studies of this species and other solitary corals (Lasker 1981; Foster et al. 1988; Goffredo et al. 2002, 2004a, 2007a; Goffredo & Chadwick-Furman 2003; Vermeij 2006). Corallite length (*L*: maximum axis of the oral disc) was measured using a caliper, and corallite mass was measured with a precision balance (after Lasker 1981; Goffredo et al. 2002; Goffredo & Chadwick-Furman 2003).

Data modeling

To obtain an objective relationship between corallite size and age, the number of annual growth bands was counted by means of computerized tomography (CT). This technique is commonly applied to scleractinian corals (Bosscher 1993; Helmle et al. 2000) and has been successfully used for *B. europaea* (Goffredo et al. 2004a). For each population, CT measurements were taken from about 40 skeletons randomly selected from the collected samples. The age of each skeleton was determined from the growth-band counts, based on one high-density band in winter and a low density band in summer (Peirano et al. 1999; Goffredo et al. 2004a; Fig. 8).

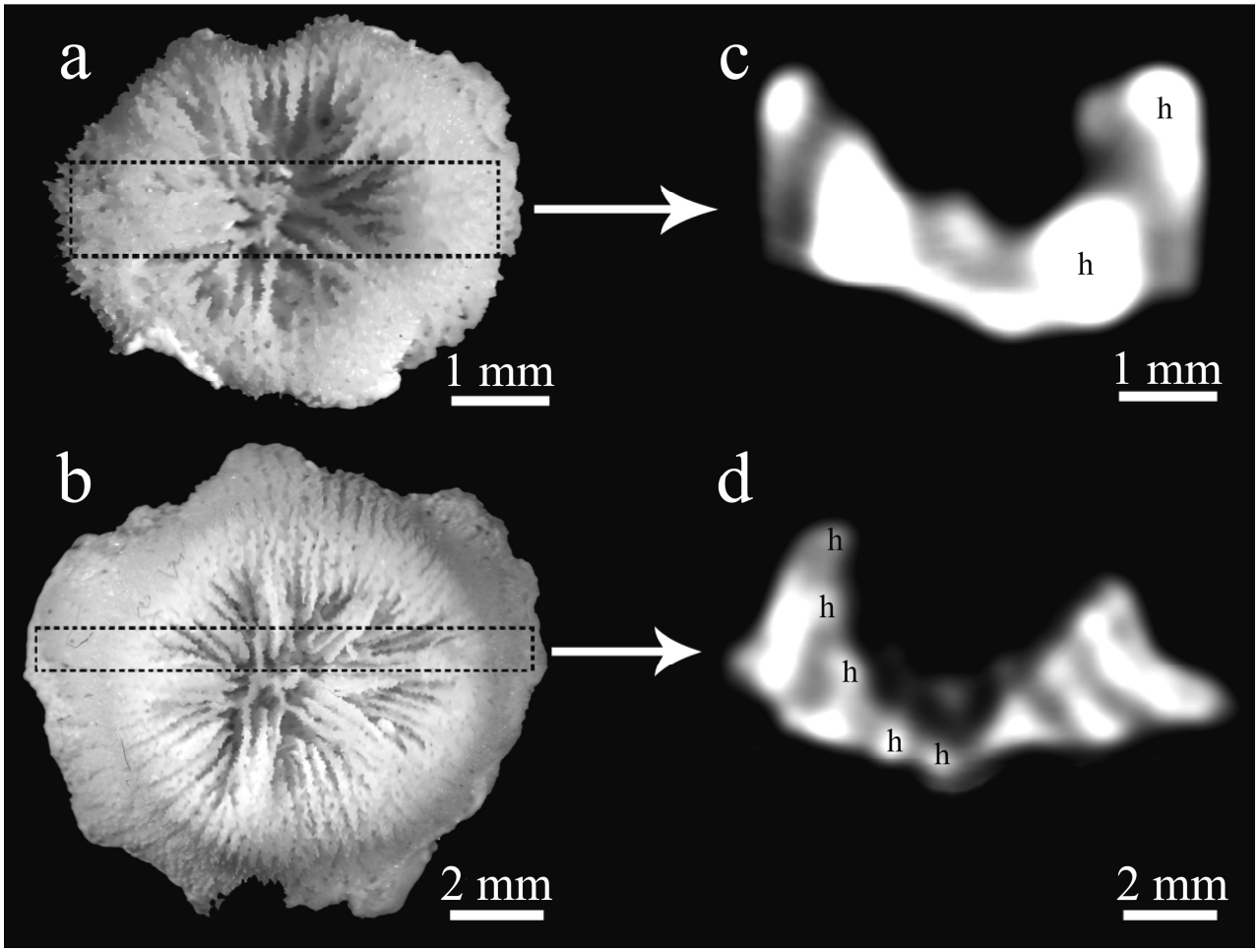

Fig. 8 *Balanophyllia europaea*. Computerized tomography scans (CT) of two corallites from the Elba island population (LB). a, b view of the skeleton from the oral pole. The dotted line shows the section, 1 mm wide, of the CT scan. The Multiple CT views facilitated the recognition of high-density bands (h). c, d sagittal CT scan (the oral pole is turned upward). Age was determined by counting the growth bands of the skeleton. c In this sample, 4.75 mm long, 2 high-density bands can be seen, corresponding to 2 years' growth. d In this sample, 9.95 mm long, 5 high-density bands can be seen, corresponding to 5 years' growth.

The von Bertalanffy growth model (von Bertalanffy 1938) predicts decreasing growth rate with age, with growth rate that tends to zero approaching an asymptotic size/age, and has been validated by Goffredo et al. (2004a) for the Calafuria (CL) population of *B. europaea* using CT density bands. To test if the von Bertalanffy function could be used for all populations sampled in this study, the decreasing growth rate of *B. europaea* with age was checked at each location (Fabens 1965). For each sample dated by CT scans, a mean growth rate was obtained by dividing length by age, and the mean growth rate was plotted against individual age (Fig. 9). All the populations showed a marked decrease of mean growth rate with age, the best fit being a negative exponential

curve (Fig. 9), from which growth was fitted to the von Bertalanffy function (von Bertalanffy 1938):

$$L_t = L_\infty (1 - e^{-Kt}) \quad (1)$$

where L_t is individual length at age t, L_∞ is asymptotic length (maximum expected length in the population), K is a growth constant (higher for a fast growth up to the asymptotic length, smaller for a slow one), and t is the age of the individual. The parameters L_∞ and K were determined by applying the "von Bertalanffy plot" method (see Pauly 1984; Sparre et al. 1989 for the exact procedure, and Goffredo & Chadwick-Furman 2003 for examples of applications to corals).

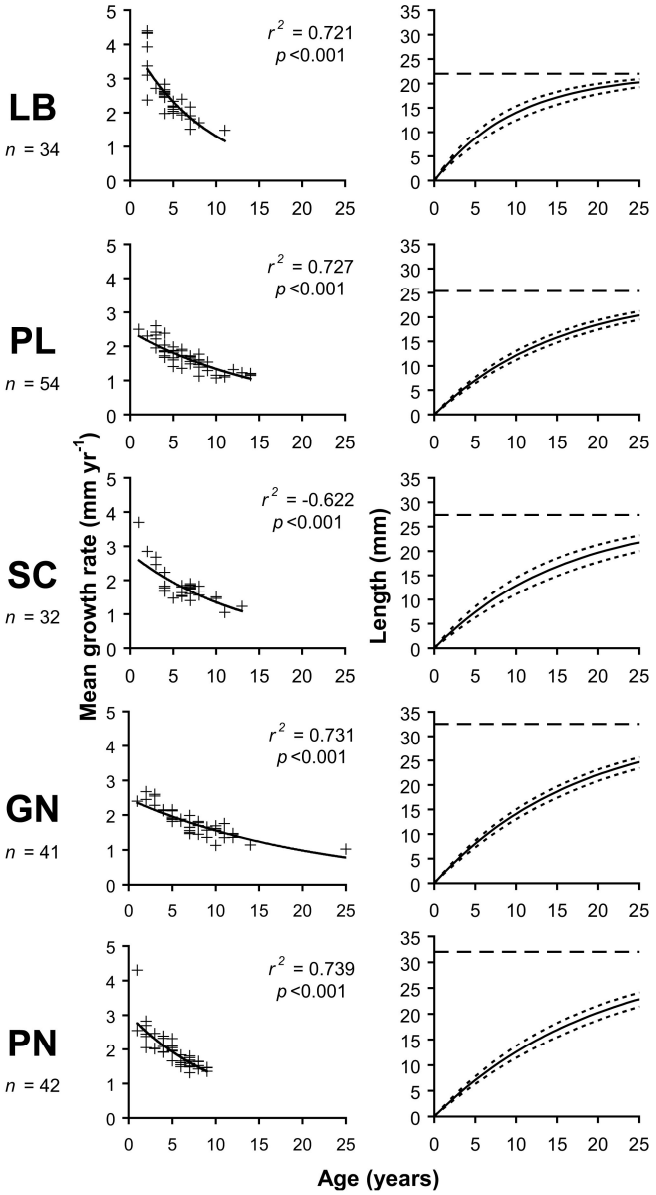

Fig. 9 *Balanophyllia europaea*. Relationships between mean growth rate and age (left hand graphs) and age-length von Bertalanffy growth curves (right hand graphs; see Equation 1) of each population with 95% confidence interval (dotted lines). The dotted horizontal line represents L_∞ value. n = number of individuals dated by computerized tomography scans (CT).

The population size structure was obtained from the survey transects, and age structure was determined using Equation 1. In a theoretical population in steady state, 100% of the variance of the frequency of age classes is explained by age. To estimate population structure stability, the age frequency distribution was analyzed using a regression analysis of the natural logarithm of the numbers of individuals (frequency) in each age class (N_t) against their corresponding age (t), or

$$\ln N_t = at + b \quad (2)$$

the slope a can be used to estimate the theoretical numeric reduction of individuals over time, the intercept b is equal to the natural logarithm of the number of individuals at age zero (N_0) (Pauly 1984; Sparre et al. 1989; Babcock 1991; Chadwick-Furman et al. 2000; Goffredo & Chadwick-

Furman 2003; Goffredo et al. 2004a). In a theoretical population in a steady state (rate of recruitment equal to rate of mortality; Grigg 1984) the coefficient of determination (r^2) is equal to unity (Beverton & Holt 1956; Pauly 1984). As natural populations deviate from the steady state, r^2 decreases to zero. In applying this method, the age classes corresponding to lengths <5 mm were ignored, since polyps this small are difficult to see during field surveys, resulting in an underestimate of these age classes (Pauly 1984; Babcock 1991; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003; Goffredo et al. 2004a). This method for estimating population stability has previously been used for colonial and solitary corals (Grigg 1984; Ross 1984; Babcock 1991; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003; Tsounis et al. 2007), including *B. europaea* (Goffredo et al. 2004a).

The slope a was used to express the theoretical numerical reduction of the corals over time (survivorship curve):

$$N_t = N_0 e^{at} \quad (3)$$

N_t is the number of individuals in each age class, N_0 is the number of individuals at age 0, a is the slope of Equation 2, t is the age.

The mean age of the individuals in each population was computed from the mean age of samples from the growth curves (Equation 1). The observed percentage of individuals below sexual maturity was obtained by summing the frequencies of the age classes below sexual maturity, which is 3-4 years (Goffredo et al. 2002, 2004a). The theoretical mean age was estimated as the mean age of the theoretical number of individuals in each population. The theoretical percentage of individuals below sexual maturity was obtained by summing the frequencies of the theoretical number of individuals of the age classes below sexual maturity in each population.

The observed biomass distribution per age class was obtained by adding the mass of each corallite in each age class. A theoretical age-mass growth curve was obtained for each population using the age-length growth curve (Equation 1) and the length-mass relationship from Goffredo et al. (2007a). The theoretical biomass distribution per age class was then obtained by multiplying the theoretical number of individuals in each age class (according to the survivorship curve, Equation 3) for the expected mass at that age. The theoretical age at maximum percentage biomass was estimated as the age class representing the highest percentage biomass. The observed age at maximum percentage biomass was determined in the same way using the observed biomass distribution. The observed mean age of biomass in the population was calculated as the sum of the products of the observed biomass in each age class multiplied by its age, then divided by the total observed biomass. This parameter estimates how old the biomass is in each population; populations with most of the biomass accumulated in younger corals will have a lower mean age of biomass

than populations in which most of the biomass is represented by older individuals. The theoretical mean age of biomass in the population was calculated in the same way, but using the theoretical biomass in each age class and the total theoretical biomass.

SST data

SST data for the years 2003-2005 were obtained for each location from the National Mareographic Network of the Agency for the Protection of the Environment and Technical Services (APAT, available at http://www.apat.gov.it). The data were from stations close to the sampling sites (< 1 km) at a depth of 1 m below minimum low tide level. Mean annual SST was computed from hourly measurements from January 2001 to January 2005 (Table 1).

Table 1 Sea surface temperature, L_∞, K and r^2 (coefficient of determination of the semi-log regression used to estimate population structure stability in Equation 2) values of the sampled populations. Growth data of the CL population from Goffredo et al. (2004a). The populations are arranged in increasing order of sea temperature.

Population	Code	SST (°C), Annual Mean (SD)	L_∞ (mm)	K	r^2
Calafuria	CL	18.023 (4.770)	21.3	0.111	0.935
Elba	LB	18.737 (5.057)	22.0	0.101	0.605
Palinuro	PL	19.138 (4.170)	25.5	0.065	0.550
Scilla	SC	19.537 (2.783)	27.4	0.063	0.503
Genova	GN	19.556 (4.723)	32.5	0.057	0.505
Pantelleria	PN	19.875 (4.766)	32.0	0.050	0.423

Statistical analyses

Analysis of covariance (ANCOVA) was used to examine differences in regression slopes and intercepts. Because of the heteroscedastic data sets, non-parametric Kruskal-Wallis was used to compare mean SST among the sites. Pearson correlation coefficients were calculated for estimating population structure stability in each population (coefficient of determination of Equation 2), and for the relationships between SST and L_∞, K, population structure stability, observed and theoretical % of individuals below sexual maturity, observed and theoretical mean age, observed and theoretical age at maximum % biomass, observed and theoretical mean age of biomass. Because of the low n value (n = 6) and the assumptions of the Pearson method, correlation coefficients were also estimated with bootstrapping (Efron 1981), with 100,000 resamples. The non-parametric Kolmogorov-Smirnov test was used to compare the age frequency distributions among the populations. All analyses were computed using SPSS 12.0, except bootstrapping (S-PLUS 6.0 Professional).

Results

Mean annual SST was significantly different between sites (Kruskal-Wallis, $p < 0.001$; Table 1). Mean growth rate was negatively related to age in all populations, with age explaining between 62 and 74% of growth rate variance (Fig. 9). Growth rates decreased from 2-5 mm yr^{-1} at ages <5 yr to 1-2 mm yr^{-1} at ages >10 yr (Fig. 9).

L_∞ and K values (Table 1) differed between the populations (ANCOVA for slope of the "von Bertalanffy plot" used to estimate L_∞ and K, $p < 0.05$). These values were therefore used to model the age-length growth curve (Equation 1) for each population (Fig. 9). L_∞ and K values were significantly correlated with SST (Table 2). SST explained more than 80% of the variance of L_∞ and more than 90% of the variance of K (Table 2).

The age of all collected individuals in the various populations was estimated using the age-length growth curves (Equation 1). The oldest individual came from the Genova (GN) population with an estimated age of 27 yr (25.65 mm length). The age-frequency distributions for each population are shown in Figure 10. The distributions were significantly different between populations (Kolmogorov-Smirnov, $p < 0.001$), and regressions of the natural logarithm of the numbers of individuals (frequency) in each age class (N_t) were computed (Equation 2; Table 1, r^2 values). These r^2 values were negatively correlated with SST (Table 2), varying from $r^2 = 0.935$ in the coldest population (CL), to $r^2 = 0.423$ in the warmest population (PN; Table 1), indicating a progressive deviation from the steady state of the populations as temperature increased (Table 2).

The theoretical percentage of individuals under sexual maturity was negatively related to SST, whilst the theoretical mean age, the theoretical age at maximum percentage biomass, and the theoretical mean age of biomass were all positively related to SST (Table 2).

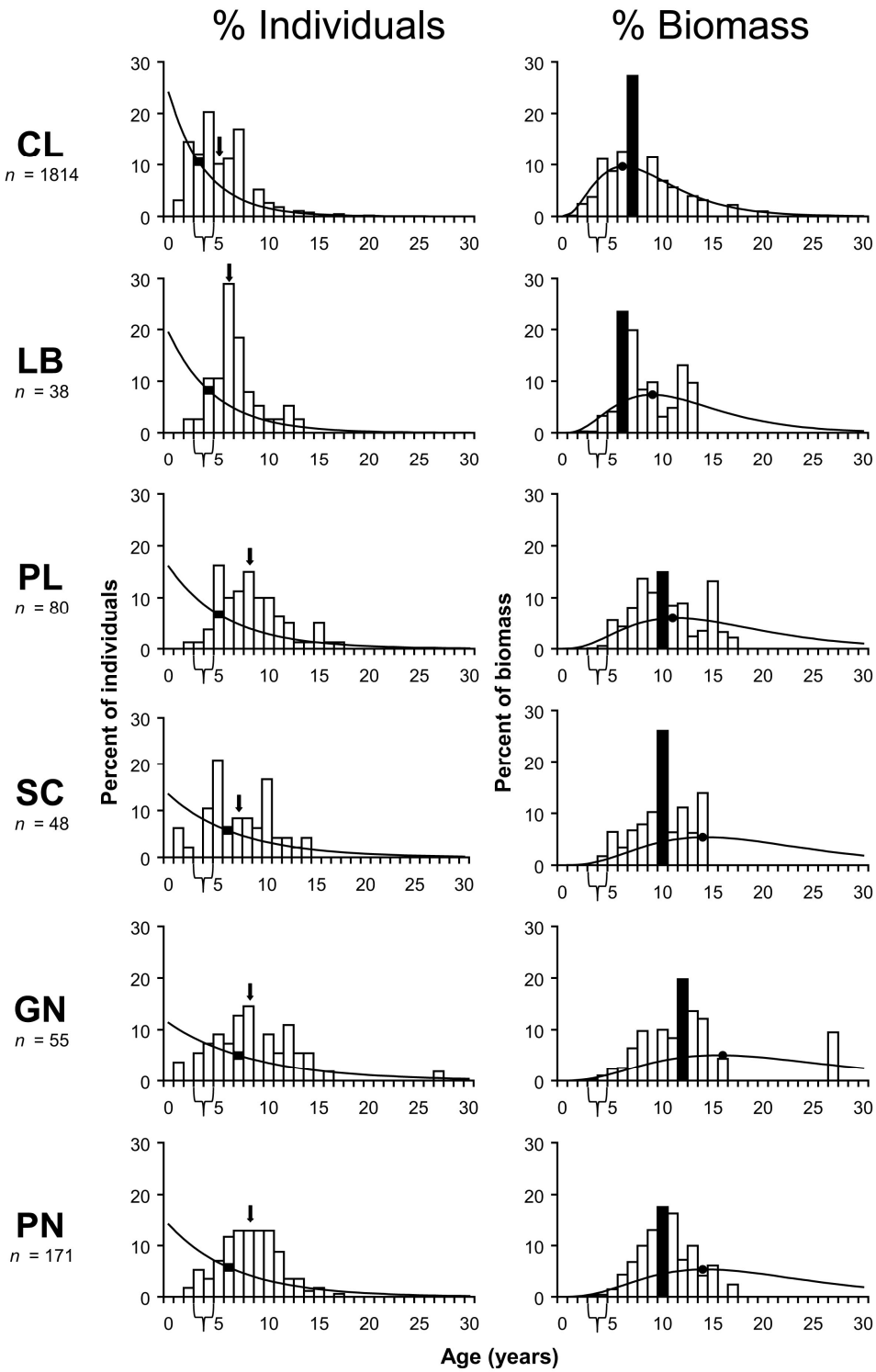

Fig. 10 *Balanophyllia europaea*. Age class structures of each population. The lines indicate the theoretical distributions. The observed (arrow) and theoretical (black square) age class containing the mean observed age of the individuals of sampled population is indicated. The observed (black column) and theoretical (black circle) age at maximum percentage biomass is indicated. Bracketed ranges indicate the age at sexual maturity. Data for the Calafuria population (CL) are from Goffredo et al. (2004a). *n* = number of individuals dated by growth curves.

Table 2 Linear regression and correlation analyses between sea surface temperature (Independent variable) and growth and demographic parameters (Dependent variable) in the sampled populations. *n* number of populations. r^2 Pearson's coefficient of determination, *r* Pearson's correlation coefficient, r^2_{BS} and r_{BS} Pearson's coefficients calculated with bootstrapping, * $p < 0.05$, ** $p < 0.01$. SE = standard error.

Dependent variable	*n*	Slope (SE)	Intercept (SE)	r^2	*r*	r^2_{BS}	r_{BS}
L_∞	6	6.373 (1.567)	-95.224 (30.018)	0.805	0.897 *	0.826	0.909 *
K	6	-0.036 (0.005)	0.757 (0.105)	0.913	-0.956 **	0.906	-0.952 **
Population structure stability	6	-0.256 (0.039)	5.486 (0.751)	0.914	-0.956 **	0.941	-0.970 **
Observed % of individuals below sexual maturity	6	-17.826 (7.266)	360.875 (139.179)	0.601	-0.775	0.310	-0.557
Theoretical % of individuals below sexual maturity	6	-12.951 (2.508)	289.102 (48.042)	0.870	-0.932 **	0.799	-0.894 *
Observed mean age	6	1.639 (0.499)	-24.062 (9.560)	0.729	0.854 *	0.548	0.740
Theoretical mean age	6	1.939 (0.488)	-31.851 (9.352)	0.798	0.893 *	0.755	0.869 *
Observed age at maximum % biomass	6	2.550 (1.046)	-39.652 (20.043)	0.598	0.773	0.588	0.767
Theoretical age at maximum % biomass	6	5.194 (0.922)	-87.777 (17.663)	0.888	0.942 **	0.846	0.920 **
Observed mean age of biomass	6	2.096 (0.775)	-30.255 (14.852)	0.646	0.804	0.605	0.778
Theoretical mean age of biomass	6	4.780 (0.566)	-77.188 (10.840)	0.947	0.973 **	0.889	0.943 **

Discussion

In zooxanthellate corals, photosynthesis enhances calcification, and both processes have temperature optima (Al-Horani 2005). It was previously hypothesized that for *Balanophyllia europaea,* inhibition of photosynthesis occurs at high temperatures, leading to a reduction in the calcification rate and skeletal density (Goffredo et al. 2007a). Also, the reduction in growth rate (*K*) with increasing temperature, highlighted in this study, might be because of a reduced energy input available for skeletal deposition, caused by the inhibition of photosynthesis in zooxanthellae.

A reduced growth rate at high temperatures has been found in the genus *Montastraea* (Carricart-Ganivet 2004), but the opposite has been reported for species of the genera *Porites* (Lough & Barnes 2000), *Acropora* and *Pocillopora* (Crossland 1981) and in mushroom corals (Goffredo & Chadwick-Furman 2003). In a study of the genera *Pocillopora*, *Acropora*, *Turbinaria*

and *Porites*, both increases and decreases in calcification with increases in temperature were reported, suggesting that the influence of temperature on growth may be species-specific (Harriott 1999). These differences might in part be due to the clade of zooxanthellae hosted by the polyp, and it has been proposed that different clades of zooxanthellae associated with corals have different environmental tolerances (e.g., light, temperature, sedimentation; Knowlton & Rohwer 2003). Under experimental conditions, zooxanthellae belonging to clade A (the clade which is hosted by most Mediterranean scleractinian corals; Visram et al. 2006), have proven to be resistant to short-term increases in temperature (Rodolfo-Metalpa et al. 2006a). However, severe bleaching episodes have been observed in situ in *O. patagonica* which also hosts clade A, in response to high temperatures (Fine et al. 2001).

In the present study the *K* growth constant was negatively correlated with SST and in an earlier study also the skeletal density was negatively correlated with SST (Goffredo et al. 2007a). On this basis, calcification would also be expected to decrease at high temperatures (calcification = extension x skeletal density; Lough & Barnes 2000; Carricart-Ganivet 2004). This is in contrast to other studies on latitudinal variations of calcification in tropical and temperate corals, where the trend was an increase in calcification with decreasing latitude (Jacques et al. 1983; Lough & Barnes 2000; Howe & Marshall 2002; Carricart-Ganivet 2004; McNeil et al. 2004). However, a recent study showed a decline of coral calcification in massive *Porites* from the Great Barrier Reef over a 16 yr period (Cooper et al. 2007), and suggested that this reduction is linked to the interactive effects of increasing seawater temperatures and pCO_2 (Reynaud et al. 2003). Calcification has an optimum temperature, and temperatures above optimum will lead to reduced calcification (Al-Horani 2005). The optimum calcification temperature for *B. europaea* may be equal to or lower than the lowest recorded temperature in this study (18.023°C), which could explain the observed decrease in calcification with increasing SST.

Despite the theoretical nature of L_∞, in growth models it is used as a measure of maximum size of individuals in the populations, and this seems to work well in *B. europaea*, fungiids and gorgonian corals (Grigg 1974; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003; Goffredo et al. 2004a; Goffredo & Lasker 2006). The increase in maximum corallite size of populations (asymptotic length) with mean SST is in agreement with previous observations, suggesting a positive correlation between biometric parameters (corallite length, width, height and volume) and temperature in *B. europaea* (Goffredo et al. 2007a). Although biologists have been interested in latitudinal variations of organism size for a long time, few studies have been conducted on marine invertebrates, and have often led to contrasting results (Lonsdale & Levinton 1985; Roy & Martien 2001; Olabarria & Thurston 2003). One of the hypotheses relating (terrestrial) body size

with latitude is based on latitudinal changes of energy availability (see Wright 1983), and predicts smaller body size at high latitudes where available energy is reduced relative to equatorial regions (Turner & Lennon 1989; Cushman et al. 1993). This theory also seems to explain the present (marine) results, since the populations characterized by higher sea temperature (i.e., higher energy) had higher individual corallite lengths. Nevertheless, the increased length is accompanied by a marked reduction in skeletal density (Goffredo et al. 2007a) and growth rate (*K*; present work). These reductions suggest that the increase in available energy, because of higher temperatures, cannot be exploited by the polyps, because of the reduced photosynthetic efficiency hypothesis (Goffredo et al. 2007a). Moreover, the increase in individual size with temperature is accompanied by a reduction in population density (Goffredo et al. 2007a), and this is in line with the hypothesis of energetic equivalence (Marquet et al. 1990), which states that, if an animal needs a certain area of space to satisfy its metabolic needs, its abundance will be inversely proportional to body size.

In a theoretical population, in a steady state, the age frequencies follow a negative exponential curve and the coefficient of determination of the semi-logarithmic regression from which *a* is estimated (Equation 2) has a value of unity (Beverton & Holt 1956; Pauly 1984). In the populations considered in this study, r^2 was negatively correlated with temperature (i.e., it deviated from the theoretical steady state value as temperature increased) reducing from 0.9 in the coldest population to 0.4 in the warmest one (Tables 1 & 2), indicating that populations characterized by high temperatures were less stable than those from lower temperatures. While some populations only had few individuals, the theoretical growth curves and the parameters derived from them were comparable with those derived from the populations with many individuals, and the derived parameters can be considered good estimates of their population characteristics. Decreasing population stability with increasing temperature is further emphasized in Table 2, where SST was correlated with almost all dependent variables. As temperature increased, the theoretical percentage of immature individuals decreased, while the theoretical mean age of individuals, the theoretical age at maximum percentage biomass, and the theoretical mean age of biomass increased, all indicating a progressive reduction in young individuals. Reduced growth and increased mortality of juvenile tropical corals as temperature increases have been reported in a case study in the US Virgin Islands (Edmunds 2004). The deficiency of younger age classes as the temperature increased might be related to recent local perturbations (e.g., excessively high temperatures) such as the 2°C increase in the maximum SST in the north west Mediterranean recorded in the year 2003, relative to the previous 50 years, and the short term increase in SST of 3-4°C relative to the mean values in the year 2003 (Rodolfo-Metalpa et al. 2006a; Diaz-Almela et al. 2007). *B. europaea* larvae are zooxanthellate and rely on the energy derived from photosynthesis (Goffredo & Zaccanti 2004), and

in zooxanthellate corals most of the energetic resources needed for gametogenesis come from photosynthesis (Rinkevich 1989). Reduced photosynthetic efficiency of zooxanthellae at high temperatures, besides limiting energetic resources for polyp gametogenesis (Rinkevich 1989; Goffredo et al. 2007a), might decrease the energy available for larvae. Together, high mortality and reduced energy might explain both the low population density (Goffredo et al. 2007a), and the reduction in numbers of young individuals with increasing temperature.

An alternative explanation for the negative effects on growth and population structure stability of *B. europaea* with increasing temperature could be related to suspension feeding. In the Mediterranean, nutrient levels and zooplankton availability are typically lower in summer-fall (i.e., high temperature) than in winter-spring (i.e., low temperature; Coma et al. 2000; Coma & Ribes 2003). Low nutrients and zooplankton availability proved to be a stress factor for corals and several benthic suspension feeding taxa (Coma et al. 2000, Coma & Ribes 2003, Peirano et al. 2005a). Moreover, in *Stylophora pistillata* colonies, starved corals present significantly lower levels of calcification and photosynthesis than fed corals (Houlbrèque et al. 2004). At high temperatures, low availability of resources would cause slow growth and low population stability in *B. europaea.* However, if this was the case, the inhibition would also be found in *L. pruvoti*, a closely related species which is totally heterotrophic but it is not. Goffredo et al. (2007a) found that skeletal and population density of *L. pruvoti* were almost the same at low and high temperature study sites, compared to *B. europaea* where they decrease at high temperature. Thus the hypothesis of photosynthetic inhibition at high temperatures seems more likely.

Global increase in sea temperature is one of the greatest threats for reef corals (Hughes et al. 2003). Rising temperatures may pose the greatest threat to populations of *B. europaea* in the warmest areas of its distribution, which could reduce the abundance of recruits. The regression between SST and theoretical percentage of individuals below sexual maturity predicts that at a mean annual SST of 22.3 °C, a population will be characterized by no immature individuals, and then will be condemned to a progressive decrease in abundance until extinction. The Intergovernmental Panel on Climate Change (IPCC) projected an increase of global SST of 1-3°C by 2100 (Solomon et al. 2007). Assuming an intermediate and rather conservative increase (2 °C), it is expected that most of the populations of *B. europaea* would be near their thermal limit (expected temperature in 2100 in the population of CL = 20.0 °C; LB = 20.7 °C; PL = 21.1 °C; SC = 21.5 °C; GN = 21.6 °C; PN = 21.9 °C). This would result in a large decrease in the input of new individuals to the population. A decrease of population density of this species with increasing SST has already been reported (Goffredo et al. 2007a).

Present evidence suggest that corals and their symbiotic zooxanthellae may be unable to acclimate or adapt fast enough to cope with the present rapid rate of water warming (Hoegh-Guldberg 1999; Hoegh-Guldberg et al. 2007). Moreover, being endemic to the Mediterranean, *B. europaea* has very limited possibilities to react to seawater warming by moving northwards toward lower temperatures, since the northern limit of the Mediterranean basin is only 1° of latitude north of the northernmost population considered in this work. The future for *B. europaea* would therefore appear to be bleak.

Chapter III

Inferred level of calcification decreases along an increasing temperature gradient in a Mediterranean endemic coral

Abstract

The correlation between solar radiation and sea surface temperature (SST) and growth was assessed along a latitudinal gradient. Extension rate and skeletal density were both correlated with calcification rate, indicating that calcium carbonate deposition was allocated evenly between skeletal density and linear extension. Unlike most studies on other tropical and temperate corals, where calcification was positively correlated with solar radiation and SST, in the present study calcification was not correlated with solar radiation, whereas it was negatively correlated with SST. I hypothesize that photosynthesis of the symbiotic algae of *Balanophyllia europaea* is inhibited at high temperatures, consequently causing an inhibition of calcification. The regressions between calcification and SST predicted that the calcification of *B. europaea* would be depressed at 20.5-21.0°C mean annual SST. The scenarios of the Intergovernmental Panel on Climate Change are that, by 2100, SST will exceed this physiological threshold for most of the populations considered in this study. This study is the first field investigation of the relationships between environmental parameters and calcification of a Mediterranean coral, and highlights risks of losing Mediterranean marine biodiversity over the next decades.

Introduction

Temperature and irradiance variations associated with latitude have an important influence on global coral distribution patterns (Kleypas et al. 1999). Latitude is the main factor influencing the variation of light and temperature (Kain 1989), which are the two environmental parameters considered in this study because they have been shown to be strongly linked to coral growth, physiology, and demography (Kleypas et al. 1999; Lough & Barnes 2000). In general, coral growth decreases with increasing latitude, to a boundary beyond 30°N and 30°S where coral reef development no longer occurs (Kinsey & Davies 1979). Coral growth is a composite of three related parameters (calcification = linear extension x skeletal density; Lough & Barnes 2000; Carricart-Ganivet 2004), and their measurement is essential when assessing the effects of environmental parameters on coral growth, because none of the three is a perfect predictor of the other two (Dodge & Brass 1984). Analyzing these variables also allows predicting the possible effect that climatic changes can have on coral ecosystems (Cooper et al. 2008). These three variables have been studied along a latitudinal gradient in the genera *Montastraea* (Carricart-Ganivet 2004) and *Porites* (Lough & Barnes 2000; Cooper et al. 2008), and variation of the three parameters has been linked to changes in temperature and light associated with latitude. In colonies of *Montastraea annularis* of the Gulf of Mexico and the Caribbean Sea, sea surface temperature (SST) is positively correlated with calcification rate and skeletal density, while it is negatively correlated with linear extension rate (Carricart-Ganivet 2004). In colonies of *Porites* of the Hawaiian archipelago, Thailand, and the Great Barrier Reef (Australia) solar radiation and SST were found to be positively correlated with calcification and linear extension rates, and negatively correlated with skeletal density (Lough & Barnes 2000). In contrast, a recent monitoring of 16 years of calcification in *Porites* colonies from the Great Barrier Reef shows that calcification declined over time, and suggests that the response may be due to the interactive effects of elevated seawater temperatures and pCO_2 increase (Cooper et al. 2008), as previously reported for colonies of *Stylophora pistillata* grown in aquaria (Reynaud et al. 2003).

Although there are numerous studies of the relationships between environmental parameters and coral growth in the tropics (Lough & Barnes 2000; Carricart-Ganivet 2004; Cooper et al. 2008), such studies are scarce for temperate zones. In *Astrangia danae* and *Plesiastrea versipora*, calcification rate increases with temperature, similar to the trend for some tropical corals, albeit over a lower temperature range (Howe & Marshall 2002). Laboratory observations on calcification rates in *Cladocora caespitosa* and *Oculina patagonica* suggest that prolonged periods of high temperatures (corresponding to or higher than the maximum summer temperature in the field) lead to a decrease of calcification (Rodolfo-Metalpa et al. 2006*b*).

This study aimed to investigate relationships between environmental parameters (solar radiation and SST) and the three growth components (calcification, skeletal density, and linear extension) in the Mediterranean coral *Balanophyllia europaea* (Risso 1826). *B. europaea* is a solitary, zooxanthellate scleractinian coral, which is endemic to the Mediterranean Sea (Zibrowius 1980). Being zooxanthellate, its distribution is limited to 0-50 m depth (Zibrowius 1980), with abundances of more than 100 individuals per square meter (Goffredo et al. 2004a). It is a simultaneous hermaphrodite and brooder (Goffredo et al. 2002). Along the Italian coasts, skeletal density and population abundance are negatively correlated with SST (Goffredo et al. 2007a). In addition, the population structures of this species become less stable and deviate from the steady state with increasing SST, due to a progressive deficiency of young individuals (Goffredo et al. 2008). In the azooxanthellate coral *Leptopsammia pruvoti*, closely related to *B. europaea* and studied in the same sites sampled in this study, no significant variation was found in the skeletal and population density with solar radiation and SST (Goffredo et al. 2007a). It has been hypothesized that temperature negatively influences the photosynthesis of the symbiotic algae of *B. europaea*, leading to negative effects on its growth and reproductive activity (Goffredo et al. 2007a, 2008). Suggested by Goreau (1959) as the 'light enhanced calcification' hypothesis, in zooxanthellate corals photosynthesis stimulates calcification, as has been confirmed in several studies (Al-Horani et al. 2005, Mass et al. 2007), and both processes have an optimal temperature (Howe and Marshall 2002). Rinkevich (1989) demonstrated the energetic contribution of photosynthetic products to coral reproduction in zooxanthellate corals.

This is the first study on the variation of the three growth components in a temperate scleractinian coral, and aims to assess the variations of calcification rate, linear extension rate, and skeletal density in populations arranged along a temperature and solar radiation gradient. The results are also considered in the light of the most recent scenarios on climate changes for the near future.

Methods

Specimens of *Balanophyllia europaea* were collected from six sites along a latitudinal gradient, from 44°20'N to 36°45'N, between 09 November 2003 to 30 September 2005 (Fig. 1). With the exception of the Calafuria population, for which data were obtained from a previous study (Goffredo et al. 2004a), samples were collected in each site using transects of at least 3 patches of 1 m^2 each, arranged in a line 5 m apart along the southern side of each reef at a depth of 5-7 m. Given the random distribution pattern of *B. europaea*, this study is not affected by the problems associated with regularly spaced quadrats and transects (Goffredo et al. 2004a). All of the polyps included

were collected from each patch. Sampling was performed at depths known to have high population densities and where the reproductive biology, biometry, population density, growth, population dynamics, and genetics of the species had previously been studied (Goffredo et al. 2002, 2004a, b). Sampling at the depth of maximum abundance may bias growth estimates toward a higher rate, and in turn underestimate age, but sampling in the chosen depth range, where 62% of the biomass of this species is found (Goffredo et al. 2004a), this bias is reduced.

Corals were dried at 50°C for 4 days and observed under a binocular microscope to remove fragments of substratum and calcareous deposits produced by other organisms. Corallite length (*L*: maximum axis of the oral disc), width (*W*: minimum axis of the oral disc) and height (*h*: oral-aboral axis) were measured with callipers and the dry skeletal mass (*M*) was measured with a precision balance. Corallite volume (*V*) was determined by applying the formula: $V = \frac{L}{2} \times \frac{W}{2} \times h\pi$ (Goffredo et al. 2007a). Skeletal density (*D*) was calculated by dividing *M* by *V*.

The age of each sample was estimated using the von Bertalanffy length-age growth functions, previously obtained for each population based on growth bands analysis by means of computerized tomography (von Bertalanffy 1938; Goffredo et al. 2008). According to the age of the polyp, the annual linear extension rate was obtained for each sample using the von Bertalanffy length-age growth functions (von Bertalanffy 1938; Goffredo et al. 2008). The mean annual calcification rate (mass of $CaCO_3$ deposited per year per area unit) was calculated for each sample by the formula: calcification (mg mm^{-2} yr^{-1}) = skeletal density (mg mm^{-3}) *x* linear extension (mm yr^{-1}) (Lough & Barnes 2000; Carricart-Ganivet 2004). Thus, for each population the mean values of skeletal density, linear extension and calcification rates of the corallites were obtained. Samples were also divided into three age classes: immature (0-4 years, after Goffredo et al. 2004a); mature (4-8 years, double the age at sexual maturity); old (>8 years).

Correlation and regression analyses between environmental and growth parameters were performed both for the full dataset and for the three age classes, to check for differences due to the different mean age of the samples in the populations (Goffredo et al. 2008). Relationships between environmental and growth parameters were performed using two models: a linear model and a power function model. The linear model was used to compare the results with other studies on environmental controls of coral growth, where linear functions are used (Lough & Barnes 2000; Carricart-Ganivet 2004). We used the power function model as it produced the best fit with the data, and to compare the results obtained by the linear model. The power function model:

$$y = ax^b \quad (4)$$

was linearized with a log-transformation of both the independent and dependent variables, producing the equation:

$$\ln(y) = b\ln(x) + \ln(a) \quad (5)$$

Sea surface temperature (SST) data for 2003-2005 were obtained for each location from the National Mareographic Network of the Agency for the Protection of the Environment and Technical Services (APAT, available at http://www.apat.gov.it). These data are measured by mareographic stations SM3810, built by the Italian Society for Precision Apparatuses (SIAP). Mean annual SST was obtained from hourly values measured from January 2001 to January 2005 (Table 1). Monthly values of solar radiation (W m^{-2}) were obtained from the International Cloud Climatology Project (ISCCP; available at http://ingrid.ldgo.columbia.edu/). These estimates are derived from satellite measurements of cloud and atmospheric optical properties. Mean annual solar radiation was obtained for the 2.5°-latitude-by-longitude square associated with each of the 6 sites (Table 1).

Because of the heteroscedastic nature of the data, the non-parametric Kruskal-Wallis test was used to compare mean solar radiation, SST, skeletal density, linear extension and calcification rates among the populations. Pearson correlation coefficients were calculated for the relationships among growth parameters and between environmental and growth parameters. Because of the low n value (n = 6) and the assumptions of the Pearson method, correlation coefficients were also estimated with bootstrapping (Efron 1981), with 100,000 resamples. All analyses were computed using SPSS 12.0, except bootstrapping (S-PLUS 6.0 Professional).

Results

Both mean annual solar radiation and SST varied significantly among the sites (Kruskal-Wallis test, $p < 0.001$; Table 1).

Mean skeletal density, linear extension and calcification rates were significantly different among the populations (Kruskal-Wallis test, $p < 0.001$; Table 3). Mean calcification rate of the corallites in the populations was positively correlated with mean linear extension rate and mean skeletal density (Table 3). Based on the bootstrapping coefficients, calcification rate explained 66% of the variance in linear extension rate and 84% of the variance in skeletal density (Table 4).

Considering the full dataset (all ages), both the linear and power function models showed that mean skeletal density of the populations was not correlated with solar radiation, while it was negatively correlated with SST, which explained 92-94% of its variance (Tables 5 & 6). Mean linear extension rate of the populations was not significantly correlated with either solar radiation or SST (Tables 5 & 6). Mean calcification rate of the populations was not correlated with solar radiation, but significantly negatively correlated with SST, which explained 74-75% of its variance

(Tables 5 & 6). The linear model indicated that a 1°C rise in SST lowered the mean skeletal density of the populations by 0.58 mg mm^{-3} and lowered the mean calcification rate of the populations by 1.00 mg mm^{-2} yr^{-1}. The trends from the whole dataset were confirmed by the age-stratified analyses on the subsets of immature and mature samples (Tables 5 & 6). The old samples subset showed a similar trend except that the mean linear extension rate of the populations was positively correlated with SST and the mean calcification rate was not significantly correlated with SST when considering the bootstrapping *r* value (Tables 5 & 6).

Table 3 *Balanophyllia europaea*. Mean skeletal density, linear extension, and calcification rates values of the populations. The sites are arranged in order of increasing SST. *n* number of individuals, SE = standard error.

Population	Code	*n*	Average skeletal density (mg mm^{-3})	SE	Average linear extension rate (mm yr^{-1})	SE	Average calcification rate (mg mm^{-2} yr^{-1})	SE
Calafuria	CL	941	1.95	0.01	1.49	0.01	2.86	0.03
Elba	LB	38	1.41	0.06	1.15	0.04	1.62	0.09
Palinuro	PL	80	1.05	0.03	0.96	0.02	1.02	0.04
Scilla	SC	48	1.01	0.04	1.12	0.03	1.12	0.06
Genova	GN	55	0.93	0.02	1.17	0.04	1.09	0.04
Pantelleria	PN	171	0.91	0.02	1.08	0.01	0.97	0.02

Table 4 *Balanophyllia europaea*. Linear regression and correlation analysis between mean skeletal density, linear extension rate, and calcification rate in the six sites ($n = 6$). r^2 Pearson's coefficient of determination, *r* Pearson's correlation coefficient, r^2_{BS} and r_{BS} Pearson's coefficients calculated with bootstrapping, * $p < 0.050$, ** $p < 0.010$, *** $p < 0.001$. SE = standard error.

Dependent variable	Independent variable	Slope (SE)	Intercept (SE)	r^2	*r*	r^2_{BS}	r_{BS}
Skeletal density	Linear extension	1.931 (0.612)	-1.034 (0.718)	0.713	0.845 *	0.392	0.626
Calcification	Linear extension	3.805 (0.795)	-2.973 (0.932)	0.851	0.923 **	0.661	0.813 *
Calcification	Skeletal density	1.773 (0.163)	-0.699 (0.206)	0.967	0.984 ***	0.841	0.917 *

Table 5 *Balanophyllia europaea*. Linear model. Linear regression and correlation analysis between environmental and growth parameters in the six sites (n = 6). Regression parameters are shown only where the relationship is significant. r^2 Pearson's coefficient of determination, r Pearson's correlation coefficient, r^2_{BS} and r_{BS} Pearson's coefficients calculated with bootstrapping, * $p < 0.050$, ** $p < 0.010$. SE = standard error.

Dependent variable	Independent variable	Slope (SE)	Intercept (SE)	r^2	r	r^2_{BS}	r_{BS}
All samples							
Skeletal density	Solar radiation	-	-	0.260	-0.510	0.244	-0.494
Linear extension	Solar radiation	-	-	0.304	-0.551	0.343	-0.586
Calcification	Solar radiation	-	-	0.278	-0.527	0.314	-0.560
Skeletal density	SST	-0.580 (0.077)	12.313 (1.475)	0.934	-0.967 **	0.920	-0.959 **
Linear extension	SST	-	-	0.527	-0.726	0.296	-0.544
Calcification	SST	-0.997 (0.209)	20.542 (4.012)	0.850	-0.922 **	0.740	-0.860 *
Immature samples (0-4 years)							
Skeletal density	Solar radiation	-	-	0.372	-0.610	0.389	-0.624
Linear extension	Solar radiation	-	-	0.493	-0.702	0.530	-0.728
Calcification	Solar radiation	-	-	0.379	-0.615	0.416	-0.645
Skeletal density	SST	-0.572 (0.121)	12.049 (2.320)	0.848	-0.921 **	0.674	-0.821 *
Linear extension	SST	-	-	0.615	-0.784	0.415	-0.644
Calcification	SST	-1.226 (0.277)	25.192 (5.300)	0.831	-0.911 *	0.667	-0.817 *
Mature samples (5-8 years)							
Skeletal density	Solar radiation	-	-	0.263	-0.513	0.329	0.574
Linear extension	Solar radiation	-	-	0.314	-0.561	0.245	-0.495
Calcification	Solar radiation	-	-	0.314	-0.561	0.318	-0.564
Skeletal density	SST	-0.643 (0.089)	13.527 (1.711)	0.928	-0.964 **	0.899	-0.948 **
Linear extension	SST	-	-	<0.001	-0.005	<0.001	-0.004
Calcification	SST	-0.766 (0.135)	16.109 (2.587)	0.890	-0.943 **	0.792	-0.890 *
Old samples (>8 years)							
Skeletal density	Solar radiation	-	-	0.206	-0.454	0.175	-0.418
Linear extension	Solar radiation	-	-	0.255	0.505	0.233	0.483
Calcification	Solar radiation	-	-	0.166	-0.408	0.105	-0.324
Skeletal density	SST	-0.704 (0.125)	14.778 (2.396)	0.888	-0.942 *	0.841	-0.917 *
Linear extension	SST	0.170 (0.012)	-2.436 (0.224)	0.981	0.991 ***	0.974	0.987 **
Calcification	SST	-	-	0.800	0.895 *	0.571	-0.756

Table 6 *Balanophyllia europaea*. Power function model (Eq. 5). Linear regression and correlation analysis between environmental and growth parameters in the six sites (n = 6) calculated on log-transformed data. Regression parameters are shown only where the relationship is significant. r^2 Pearson's coefficient of determination, r Pearson's correlation coefficient, r^2_{BS} and r_{BS} Pearson's coefficients calculated with bootstrapping, * $p < 0.050$, ** $p < 0.010$, *** $p < 0.001$. SE = standard error.

Dependent variable	Independent variable	Slope (SE)	Intercept (SE)	r^2	r	r^2_{BS}	r_{BS}
All samples							
Skeletal density	Solar radiation	-	-	0.252	-0.502	0.230	-0.480
Linear extension	Solar radiation	-	-	0.318	-0.564	0.352	-0.593
Calcification	Solar radiation	-	-	0.316	-0.562	0.333	-0.577
Skeletal density	SST	-8.162 (0.876)	24.241 (2.586)	0.956	-0.978 ***	0.935	-0.967 **
Linear extension	SST	-	-	0.488	-0.698	0.289	-0.538
Calcification	SST	-10.932 (1.981)	32.551 (5.848)	0.884	-0.940 **	0.752	-0.867 *
Immature samples (0-4 years)							
Skeletal density	Solar radiation	-	-	0.407	-0.638	0.408	-0.639
Linear extension	Solar radiation	-	-	0.516	-0.718	0.540	-0.735
Calcification	Solar radiation	-	-	0.452	-0.672	0.460	-0.678
Skeletal density	SST	-8.829 (2.073)	26.095 (6.120)	0.819	-0.905 *	0.661	-0.813 *
Linear extension	SST	-	-	0.050	-0.224	0.411	-0.641
Calcification	SST	-11.503 (2.943)	34.396 (8.687)	0.792	-0.890 *	0.659	-0.812 *
Mature samples (5-8 years)							
Skeletal density	Solar radiation	-	-	0.274	-0.523	0.248	-0.498
Linear extension	Solar radiation	-	-	0.314	-0.560	0.324	-0.569
Calcification	Solar radiation	-	-	0.353	-0.594	0.347	-0.589
Skeletal density	SST	-9.007 (0.918)	26.730 (2.710)	0.960	-0.980 ***	0.922	-0.960 **
Linear extension	SST	-	-	<0.001	-0.015	<0.001	-0.016
Calcification	SST	-8.936 (1.431)	26.685 (4.224)	0.907	-0.952 **	0.799	-0.894 *
Old samples (>8 years)							
Skeletal density	Solar radiation	-	-	0.191	-0.437	0.167	-0.403
Linear extension	Solar radiation	-	-	0.246	0.496	0.229	0.479
Calcification	Solar radiation	-	-	0.152	-0.390	0.097	-0.311
Skeletal density	SST	-8.980 (1.316)	26.713 (3.885)	0.921	-0.960 **	0.857	-0.926 **
Linear extension	SST	4.127 (0.268)	-12.382 (0.792)	0.983	0.992 ***	0.974	0.987 ***
Calcification	SST	-	-	0.798	-0.893 *	0.570	-0.755

Based on the two significant regressions from the whole dataset, the linear model predicted that calcification would have ceased at a mean annual SST of 20.5°C and the skeletal density would fall to zero values at a mean annual SST of 21.2°C (Table 5). The power function model predicted that calcification would have approached zero values at 21.0°C and the skeletal density would have approached zero values at a mean annual SST of 21.3°C (Table 6).

Discussion

The 'stretching modulation of skeletal growth' is a mechanism that corals can adopt for preferentially investing calcification in skeletal density or linear extension (Carricart-Ganivet & Merino 2001; Carricart-Ganivet 2004). *Porites*, for example, invests increased calcification at higher temperatures into linear extension, allowing the coral to occupy space as rapidly as possible (Lough & Barnes 2000). In contrast, *Montastraea annularis* invests increased calcification at higher temperatures to construct denser skeletons (Carricart-Ganivet & Merino 2001; Carricart-Ganivet 2004). In *Balanophyllia europaea*, linear extension rate and skeletal density were both positively correlated with calcification rate, indicating that the capacity to colonize the substratum quickly and the mechanical strength of the skeleton are both important for this species, and that calcification is allocated evenly between increasing skeletal density and linear extension, in comparison with *Porites* and *M. annularis*. For each 1 mg mm^{-2} yr^{-1} of calcification rate reduction, linear extension rate decreased by ~ 0.3 mm yr^{-1} and skeletal density decreased by ~ 0.6 mg mm^{-3}.

Calculated density values were reasonable with respect to other studies on tropical species (Bucher et al. 1998; Lough & Barnes 2000; Carricart-Ganivet 2004). The geometrically computed skeletal density used in this and in previous studies (Goffredo et al. 2007a) is analogous to the bulk density (Bucher et al. 1998), which is equal to the skeletal mass divided by the total volume (skeletal matrix volume plus pores volume; Bucher et al. 1998). Skeletal matrix volume is further composed by the $CaCO_3$ and by the intracrystalline organic framework regulating the crystallization process (Cohen & McConnaughey 2003). Analyses to quantify the organic framework content and porosity in the same samples are currently underway, to verify if the variation in bulk skeletal density depends on the porosity or on the specific gravity of $CaCO_3$ crystals or on the content of organic framework. Estimates of micro-density may be obtained by a water displacement technique, but we chose not to use this method because the procedure involves the use of acetone (Bucher et al. 1998), and could have affected the above-mentioned fine studies on organic framework quantification.

The fact that calcification rate and skeletal density were not correlated with solar radiation, while they were negatively correlated with SST, confirms previous studies on the biometry, growth and population structure stability of this species, where the coral parameters show stronger and more significant relationships with temperature than with light (Goffredo et al. 2007a, 2008). For both the linear and power function models, trends of the analyses performed on the full dataset were confirmed by most of the analyses on the three age-based subsets, indicating that differences in the mean age of the samples in the populations (Goffredo et al. 2008) did not bias the results. The positive correlation between linear extension rate and SST in the older samples is expected, since

corallite asymptotic length in the populations is positively correlated with SST. Given the reduced growth rate of this species as corallite size approaches the asymptotic one, old samples in cooler waters are close to their asymptotic length and extend their size very slowly, while old samples in warmer waters are far from the asymptote and still significantly increase their size (Goffredo et al. 2008). This is very likely the cause of the lowered *r* value in the negative correlation between calcification and SST for the old samples subset (i.e., linear extension in the old samples subset do not decrease with SST as in the other subsets, and the decrease of calcification with SST is less steep).

The decrease in calcification rate with increasing temperature for *B. europaea* is in contrast with other studies on latitudinal variations of calcification in tropical and temperate corals, where the trend was the opposite (Lough & Barnes 2000; Howe & Marshall 2002; Carricart-Ganivet 2004). Besides being opposite, the response of *B. europaea* calcification rate to temperature (-1.00 mg mm^{-2} yr^{-1} $°C^{-1}$; present work, Table 5) was three times lower than that of *Porites* (+3.30 mg mm^{-2} yr^{-1} $°C^{-1}$; Lough & Barnes 2000), and five times lower in comparison with *Montastraea annularis* (+5.70 mg mm^{-2} yr^{-1} $°C^{-1}$; Carricart-Ganivet 2004). However, a recent study shows a decline of coral calcification in massive *Porites* from the Great Barrier Reef over a 16-year period (Cooper et al. 2008), and suggests that this reduction is linked to the interactive effects of increasing seawater temperatures and pCO_2 associated acidification (Reynaud et al. 2003).

The reduction of *B. europaea* calcification with increasing temperature might depend on the response of zooxanthellae photosynthesis to temperature, since in zooxanthellate corals calcification is enhanced by photosynthesis (Al-Horani et al. 2005), and both processes have temperature optima (Howe & Marshall 2002). In the closely related non-photosynthetic coral *Leptopsammia pruvoti* the skeletal density measured in the same localities of this study is not affected by temperature (Goffredo et al. 2007a). Moreover, linear extension rate and calcification are not significantly different between two populations of *L. pruvoti* 850 km apart, despite the different thermal regimes (S. Goffredo et al. unpubl.). Preliminary studies of various populations of *B. europaea* have found zooxanthellae belonging exclusively to clade A (M. A. Coffroth pers. comm.), as previously reported for one population in Spain (Visram et al. 2006). Under experimental conditions, zooxanthellae belonging to this clade hosted by *Cladocora caespitosa* have proved to be resistant to short term temperature increases, even above those recorded in nature (Rodolfo-Metalpa et al. 2006a). However, exposure to the same temperature range for prolonged periods has been lethal for 100% of the colonies of *C. caespitosa* studied (Rodolfo-Metalpa et al. 2006b). In situ, several mass mortality events have been reported for *B. europaea* and *C. caespitosa*, linked to periods of elevated temperatures and zooxanthellae bleaching (Rodolfo-Metalpa et al. 2000). The optimal temperature

for the photosynthesis of *B. europaea* symbiotic system might be equal to or lower than the lowest ever recorded in nature in the populations sampled in this study (18.0°C). Testing the hypothesis that a rise in temperature causes a significant reduction in the photosynthetic efficiency of clade A zooxanthellae in *B. europaea* requires further investigations by experimental approaches (Karako-Lampert et al. 2005; Rodolfo-Metalpa et al. 2006a, b).

Energetic constraints related to suspension feeding may provide an alternative explanation for the negative effects of increasing temperature on calcification of *B. europaea*. In the Mediterranean, the warm summer-fall season is characterized by lower nutrient levels and zooplankton availability than the cool winter-spring season (Coma et al. 2000). Corals and several benthic suspension feeding taxa have proved to be stressed by low nutrients and limited zooplankton availability (Coma et al. 2000). In *Stylophora pistillata* colonies, starved corals show significantly lower levels of calcification and photosynthesis than fed corals (Houlbrèque et al. 2004). Low availability of resources at high temperatures may slow calcification in *B. europaea.* However, if this was the case, the inhibition would also be found in the azooxanthellate, non-photosynthetic species *L. pruvoti*. Instead, *L. pruvoti* demography seems to be unaffected by temperature (Goffredo et al. 2007a). Although the hypothesis of photosynthetic inhibition at high temperatures is intriguing, other environmental parameters may influence coral growth (pH, total alkalinity, wave exposition, flow rate, etc.), and contribute in producing the observed trends. Further investigation are needed to better constrain the environmental controls on the growth of this species.

My results encourage speculations of the possible effect of global climate change on this species. Global increase in sea temperature is one of the greatest threats for reef corals (Hughes et al. 2003). The linear regression between calcification rate and SST predicted that calcification of *B. europaea* would cease at a mean annual SST of 20.5°C (zero values of skeletal density would occur at 21.2°C). When considering the power function model, calcification is expected to approach 0 values at 21.0°C (21.3°C for the skeletal density), values very close to the ones obtained by the linear model. Extrapolating the regressions between calcification and SST has the limitation of assuming that the linear (or power function) relationship will be maintained. This may not necessarily be true, in fact, while from 18.0°C (CL) to 19.1°C (PL) calcification drops by 64% (2.86 to 1.02 mg mm^{-2} yr^{-1}), from 19.1°C (PL) to 19.9°C (PN) it drops only by 5% (1.02 to 0.97 mg mm^{-2} yr^{-1}), suggesting the existence of a possible plateau (Table 5). Using a power function model partially addressed this problem, but the limits of extrapolating beyond the warmest temperature recorded remain. The conclusions must be taken with caution, but the concern for the possible negative fate of this endemic species with continued global warming remains. While adaptive

changes such as acclimation (modifying cell metabolism to perform better at the new temperatures) or adaptation (the selection of organisms that respond better to the new temperatures; Clarke 1983) can not be excluded as SST rises, evidence that corals and their symbionts can adapt to rapid climate change is equivocal or nonexistent (Hoegh-Guldberg et al. 2007). Global SSTs are projected to increase by 1-3°C by 2100, with a higher increase in temperate areas of the northern hemisphere than in tropical areas (Solomon et al. 2007). Assuming an intermediate and rather conservative increase (2°C), SST is expected to approach the zero calcification point for most of the populations considered in this study (projected temperature in 2100 in the population of Calafuria = 20.0°C; Elba = 20.7°C; Palinuro = 21.1°C; Scilla = 21.5°C; Genova = 21.6°C; and Pantelleria = 21.9°C). This scenario would suggest a possible reduction in the distribution area of this species, with irrecoverable losses of genetic variability, considering the fragmented genetic structure that characterizes the species (Goffredo et al. 2004b). At the same time, the fragmented genetic structure suggests that changes from one latitude to another may involve genetic differences between locally adapted corals, and corals used in our study may have had an untold number of years to adapt to the average annual temperature at their site (Kleypas et al. 2005). This may have biased my approach of using a spatial relationship to infer how populations will respond to future temperatures. Studies have shown that corals can adapt if given thousands of years, but the IPCC scenarios we considered are on a timescale of one order of magnitude shorter, and this could give no chances for adaptation. To produce a more accurate projection of future calcification rates in response to increased temperature, physiological experimental studies of the calcification-temperature relationships in corals from the various populations under current-seasonal and future-expected temperatures are needed. Even then, we cannot be sure that corals couldn't adapt if given 50-100 years since little is known about rates of adaptation.

This study is the first field investigation of the relationship between environmental parameters and estimated growth parameters of a Mediterranean coral. Being endemic to the Mediterranean, *B. europaea* has very limited possibilities to respond to seawater warming by moving northwards toward lower temperatures, since the latitudinal range considered covers almost the entire northern distribution of this species. Even with the limits of curve extrapolation, this study highlights the risk of losing Mediterranean marine biodiversity over the next decades, adding a voice to the choir of scientists that for years have been asking for a worldwide political intervention to slow down global warming.

Chapter IV

Growth and population dynamic model of the non-zooxanthellate temperate solitary coral *Leptopsammia pruvoti* (Scleractinia, Dendrophylliidae)

Abstract

In corals where complex life history processes decoupling age from size are rare or clearly detectable, individual age may be determined from size, and age-based growth and population dynamic models may be applied. Population size and structure, and growth rates of *Leptopsammia pruvoti* were determined at Calafuria, Ligurian Sea. Growth rate decreased with increasing size. The growth curve derived from field measurements matched the one obtained by growth bands analysis. The frequency of individuals decreased exponentially with age, indicating a steady state population. Turnover time was 2.3 years. Maximum lifespan was 13 years. Most reproductive output was from intermediate age classes, while older individuals, although having higher fecundity, were rare and accounted for a minority of population reproductive output. In comparison with other solitary dendrophylliids, *L. pruvoti* evolved a mixed life strategy, with reproduction characterized by *r*-strategy correlates, and rate of demographic renewal occurring halfway along the *r*–*K* continuum.

Introduction

Demographic analysis of coral populations may reveal the extent to which they are under stress, and is especially useful when anthropogenic activities disturb reefs and threaten the viability of coral populations (Grigg 1984; Guzner et al. 2007). In addition, the development of restoration strategies for damaged or degraded coastal areas requires information on population turnover (Chadwick-Furman et al. 2000; Epstein et al. 2001; Goffredo & Chadwick-Furman 2003).

Studies that quantify life-history parameters of corals are few. The scarce studies on population dynamics of scleractinian corals were reviewed around 35 years ago, describing their growth and survivorship (Connell 1973). Since then, demographic processes have been described for some species in the Red Sea (Loya 1976; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003; Glassom & Chadwick 2006; Guzner et al. 2007), Pacific (Fadlallah 1983; Nozawa et al. 2008), Southwestern Atlantic (Lins de Barros & Pires 2006), Caribbean (Hughes & Jackson 1985; Johnson 1992; Meesters et al. 2001; Vermeij et al. 2007), Great Barrier Reef (Babcock 1991), and the Mediterranean (Goffredo et al. 2004a, 2008; Shenkar et al. 2005). Processes of fragmentation, fusion and partial colony mortality of scleractinians, causing corals of similar size to be of widely different ages, distort the age-size relationships, and this may partly explain the paucity of information on population dynamics of this group (Hughes & Jackson 1985; Babcock 1991). These phenomena, characteristic of clonal modular organisms (Hughes 1989), prevent the application of traditional age-based growth and population dynamic models and create highly complex demographic patterns (Hughes & Jackson 1985). The growth of modular individuals can be modeled through the replication, growth and death of the modules (Harper 1977), and studies of modular growth have often focused on plasticity of form and the complexity of both individual colony growth and population dynamics of modular organisms (Hughes & Jackson 1985; Hughes 1989; Babcock 1991). Due to this complexity, an analysis of 13 Caribbean coral species used a size-based, rather than age-based, assessment of population structure (Meesters et al. 2001), and recently new size-structured models for coral growth and population dynamics have been proposed (Artzy-Randrup et al. 2007).

In species in which fragmentation or fusion of individuals are rare, and partial mortality can be recognized by anomalies in the regular growth pattern, coral age can be determined (Babcock 1991; Chadwick-Furman et al. 2000). The growth and dynamics of some modular organisms can be examined using age-based models thanks to one of their emergent properties: colony form (Grigg 1977, 1984; Goffredo & Lasker 2006). In addition, in some solitary corals, age estimates may be easily obtained from externally visible growth bands (Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003). Growth band analysis has been widely used to determine the age of

colonial scleractinian and gorgonian corals (Knuston et al. 1972; Logan & Anderson 1991; Goffredo & Lasker 2006). Thus, growth and population dynamic models based on age can be applied to certain coral growth forms to describe demographic characteristics (Grigg 1984; Ross 1984; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003). Recently, the age-based Beverton-Holt model provided an adaptive management approach for regulating an octocoral fishery for bioactive compounds in the Bahamas, avoiding long-term characterization of population dynamics which is rarely available (Goffredo & Lasker 2008).

Leptopsammia pruvoti Lacaze-Duthiers, 1897 is an ahermatypic, non-zooxanthellate, and solitary scleractinian coral, which is distributed in the Mediterranean basin and along the European Atlantic coast from Portugal to Southern England and Ireland (Zibrowius 1980). It is one of the most common organisms in semi-enclosed rocky habitats, under overhangs, in caverns, and small crevices at 0–70 m depth, with mean population abundances of more than ten thousand individuals per square meter, i.e. more than two kilograms of $CaCO_3$ biomass m^{-2} (Goffredo et al. 2007a). Sea surface temperature and solar radiation do not significantly influence its biometry (skeletal density, corallite length, width, and height) or population abundance along an 850 km latitudinal gradient in Western Italian coasts (Goffredo et al. 2007a). It is a gonochoric internal brooder (Goffredo et al. 2006). Fertilization takes place from January to April and planulation during May and June. When released, the planula larvae have completed ontogenesis, have a size of 695–1,595 μm in length, and under laboratory rearing conditions, swim by ciliary movement for several days (Goffredo et al. 2005). Evidence of asexual reproduction (either through polyp budding or fission) has not been observed (Goffredo et al. 2006, and reference therein). Its genetic structure markedly departs from Hardy-Weinberg equilibrium, with a considerable deficit of heterozygotes at all scales, from patch to populations. Most genetic differentiation occurs between patches within populations, rather than among distant populations, with no significant correlation between genetic differentiation and geographic distance (Goffredo et al. 2009). Its yellow color and high abundance make this species attractive to recreational divers, who represent an important income for coastal tourist resorts in the Mediterranean (Mundet & Ribera 2001).

The purpose of this study is to describe the population dynamics of *L. pruvoti* in the Eastern Ligurian Sea, by applying the Beverton & Holt population dynamic model based on age (Beverton & Holt 1957; Chadwick-Furman et al. 2000; Goffredo & Lasker 2008). This report completes the description of life history strategy of this temperate coral in the Mediterranean Sea, together with previous studies on reproductive biology, environmental correlates of demographic characteristics, and genetic differentiation (Goffredo et al. 2005, 2006, 2007a, 2009). The questions addressed in this study are: 1) Do the growth bands of *L. pruvoti* reflect the growth pattern in the field? 2) Which

indications about population conditions can be drawn by the population dynamics of this species at Calafuria? 3) What is the life history strategy of this species compared to other related corals? This is only the second solitary coral to be examined for demographic patterns in the Mediterranean Sea, and only the third world-wide in temperate ecosystems. Thus, this description represents a substantial advance in the sparse literature on the dynamics of cold-water corals.

Materials and methods

The study population of *Leptopsammia pruvoti* was located off the coast of Calafuria (10 km south of Livorno, Italy, Eastern Ligurian Sea, NW Mediterranean, 43°28'N, 10°20'E; see Goffredo et al. 2004a for description of study site; Fig. 1). The growth rate of 38 individuals of *L. pruvoti*, marked in situ by numbered plastic tags nailed to the rock, at a depth of 16 m, was measured from December 2007 to June 2009. The length (*L*: maximum axis of the oral disc) and width (*W*: minimum axis of the oral disc) of each marked polyp were measured in situ with calipers (±0.5 mm) every 3 months for 0.2-1.5 years (average: 1.0 years). The period of measurement varied among individuals because corals that died (8 during the whole study, of different size) were replaced by others of similar size during the study. Corals were sampled at depths known to have high population abundance and at the same depth as that of previous studies on the reproduction, biometry and population abundance of this species (Goffredo et al. 2005, 2006, 2007a). Three digital thermometers (i-Button DS1921L-F52, Maxim Integrated Products, Dallas Semiconductors) were placed in the experimental field to record seawater temperature at intervals of 2 hours during the study period. Thermometers were replaced every 3 months to download data and avoid problems of encrustation and overgrowth by marine organisms.

To obtain an additional measure of the relationship between polyp size and age, for comparison with that obtained from field measurements of growth rates, the number of annual growth bands on selected individuals was counted by means of computerized tomography (CT, after Logan & Anderson 1991; Goffredo et al. 2004a, 2008). Specimens used in CT measurements (n = 29) were collected at Calafuria at 16 m depth near the individuals that were marked for in situ growth measurements. Coral length, width and dry skeletal mass (*M*) were measured (Goffredo et al. 2007a), and age was determined from growth band counts, based on the pattern in temperate and semi-temperate corals of deposition of two bands per year, a high-density band in winter and a low-density band in summer (Peirano et al. 1999; Goffredo et al. 2004a, 2008; Goffredo & Lasker 2006, 2008).

Growth rates based on both the size–age data from CT, and the directly observed growth rates, were fit to the Von Bertalanffy function (Von Bertalanffy 1938):

$$L_t = L_\infty (1 - e^{-Kt}) \quad (1)$$

where L_t is individual length at age t, L_∞ is asymptotic length (maximum expected length in the population), K is a growth constant, and t is individual age. The parameters L_∞ and K were determined by applying the "Gulland and Holt plot" (for field data) and "Ford–Walford plot" (for growth bands data) methods (see Pauly 1984; Sparre et al. 1989 for the exact procedure, and Goffredo & Chadwick-Furman 2003; Goffredo et al. 2004a, 2008; Goffredo & Lasker 2006 for examples of application to corals). Only a single growth rate summarizing growth over the entire observation period was used for each coral. All growth rates were normalized to one year.

Population size structure was derived from a transect dataset from Calafuria obtained during previous work (Goffredo et al. 2007a), and age structure was determined using the von Bertalanffy age-length function (Eq. 1). The instantaneous rate of mortality (Z) of the population was determined by an analysis of the age frequency distribution (see Pauly 1984; Sparre et al. 1989; Babcock 1991; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003; Goffredo et al. 2004a, 2008). This estimation of mortality rate implies a steady state for the population, requiring an age structure characterized by a decreasing "monotonic" pattern with each age class greater than the next, and it has broadly been used for colonial and solitary corals (Grigg 1984; Babcock 1991; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003; Goffredo et al. 2004a; Goffredo & Lasker 2008). The instantaneous rate of mortality was then used to express the numeric reduction of the corals over time (survivorship curve):

$$N_t = N_0 e^{-Zt} \quad (3)$$

where N_t is the number of individuals at age t, N_0 is the number of individuals at age 0, Z is the instantaneous rate of mortality and t is individual age measured in years. The turnover time, equivalent to the mean lifespan, was calculated as the reciprocal of Z (see Pauly 1984; Goffredo & Chadwick-Furman 2003; Goffredo et al. 2004a). Maximum lifespan was calculated as the age at which <0.5% of the population was still surviving, based on survival curves (see Sparre et al. 1989; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003).

The age-based length growth curve was converted into a dry skeletal mass growth curve using the skeletal length-mass relationship for this species at this site and depth (Goffredo et al. 2007a). Using the Beverton and Holt model (Beverton & Holt 1957), an age-specific curve expressing cohort yield in dry skeletal mass was generated using the growth curve of coral dry skeletal mass and the survivorship curve (i.e. cohort yield at age t = individual dry skeletal mass at age t x survivorship at age t; see Grigg 1984; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003; Goffredo et al. 2004a).

The sex ratio, average fecundity (number of planulae produced per unit body volume), and percent fertile individuals in each age class all were derived from previous work (Goffredo et al. 2006), and planula production in each age class of *L. pruvoti* at Calafuria was estimated (Table 7). Planula production integrated fecundity (b_i), number of individuals (X_i), sex ratio (SR) and fertility (F_i) in each age class, thus planula production = b_i X_i SR F_i, all estimated from the population.

Table 7 *Leptopsammia pruvoti.* Life table constructed for the Calafuria population. X_i = abundance of individuals (N m^{-2}) estimated by the equation $\ln(N_t) = -0.427 \cdot t + 4.339$ (over 128 cm^2 of surface area, r^2 = 0.839; $p < 0.001$; see results); b_i = average fecundity of female polyps (planulae per female polyp), F_i = percentage of fertile individuals (derived from Goffredo et al. 2006); b_i X_i = number of planulae produced by each age class. Considered sex ratio was 1:1 (Goffredo et al. 2006). Data refer to a 1 m^2 area. Values in brackets are the 95% confidence intervals.

Life history trait	Age class (i)	X_i	b_i	F_i	b_i X_i
	0	6004 (2532-14235)	0	0.00	0
	1	3918 (1925-7977)	0	0.00	0
Sexual maturity	**2**	**2557 (1463-4470)**	**12 (6-19)**	**0.50**	**7969 (2194-21233)**
	3	1669 (1112-2505)	37 (19-56)	0.65 (0.54-0.77)	20371 (5705-54009)
	4	1089 (845-1404)	75 (38-112)	0.78 (0.75-0.82)	32192 (12041-64472)
	5	711 (642-787)	123 (63-183)	0.88 (0.85-0.90)	38315 (17190-64809)
Maximum planula Production	**6**	**464 (441-488)**	**176 (90-263)**	**0.94 (0.87-1.00)**	**38598 (17265-64172)**
	7	303 (247-371)	232 (118-345)	0.99 (0.89-1.00)	34884 (12970-63998)
	8	198 (138-282)	287 (146-427)	1.00 (0.90-1.00)	28320 (9067-60207)
	9	129 (78-214)	338 (173-504)	1.00 (0.91-1.00)	21828 (6140-53928)
	10	84 (43-163)	386 (197-575)	1.00 (0.92-1.00)	16262 (3897-46863)
	11	55 (24-124)	430 (219-640)	1.00 (0.93-1.00)	11803 (2444-39680)
	12	36 (14-94)	468 (239-697)	1.00 (0.94-1.00)	8394 (1573-32759)
Maximum longevity	**13**	**23 (8-71)**	**502 (256-748)**	**1.00 (0.94-1.00)**	**5874 (963-26554)**
Total		17241 (9512-33185)	-	-	264810 (91449-592684)

Reliability tests for length-age predictions, that is the Cronbach's Alpha coefficient (Cronbach 1951) and the Intraclass Correlation Coefficient (Burch 2009), were calculated with SPSS 12.0.

Results

Growth rate and life time growth curve

The length of *Leptopsammia pruvoti* was chosen as the primary biometrical measurement because it provided the best fit to dry skeletal mass (r^2 = 0.924; see Goffredo et al. 2007a).

Observed growth rates provided estimates of growth over the full size range of *L. pruvoti* individuals (Fig. 11). Growth rate decreased as a function of coral length. On average, individuals ranging from 2 to 4 mm in length grew 1.0 mm per year (SE = 0.2; n = 17), individuals ranging from 4 to 6 mm in length grew 0.7 mm per year (SE = 0.1; n = 18), while individuals ranging from 6 to 8 mm in length grew 0.3 mm per year (SE = 0.4; n = 3). The average growth rate was significantly different among size classes (ANOVA, $P < 0.001$). The growth rates of *L. pruvoti* individuals at Calafuria were also markedly variable within size groups (coefficient of variation within size classes = 70-190%). The regression of growth rate against coral length, although significant (p = 0.026), explained only 13.1% of the total variance in growth rates.

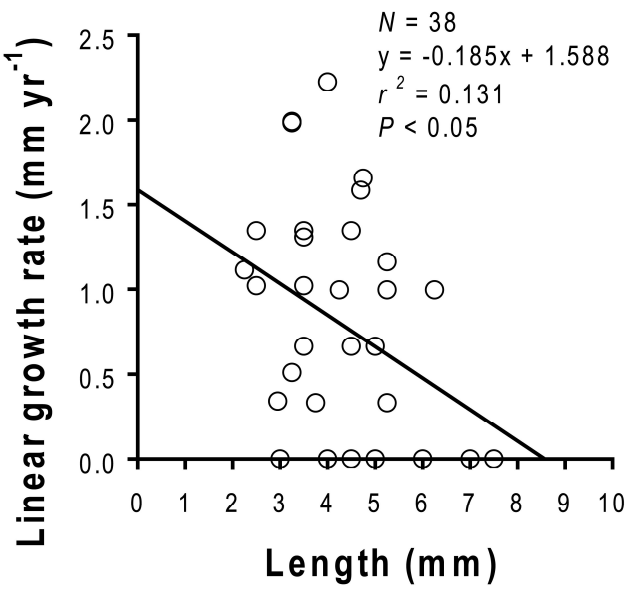

Fig. 11 *Leptopsammia pruvoti*. Variation in linear growth rate from in situ field measurements of individual corals during 0.2-1.5 years on a rocky reef at Calafuria, Eastern Ligurian Sea, at a depth of 16 m. This plot corresponds to the Gulland and Holt plot for the estimation of von Bertalanffy Growth function parameters K and L_∞. The observations are independent; i.e. a separate individual is represented by each data point. The ordinate is size increment per unit time, and the abscissa is mean size for the increments in question.

The variation of growth data could have been increased by the variation in the duration of field measurements of growth rates (Table 8), and by the mean seasonal temperature differences, which may span 7 degrees (mean winter/spring temperature = 13.6 °C, range = 13-15 °C; mean

summer/fall temperature = 21.4, range = 19-26 °C). According to the Gulland and Holt plot method, the population had a growth constant $K = 0.185$ and a maximum expected length $L_\infty = 8.6$ mm (Fig. 11).

Table 8 *Leptopsammia pruvoti.* Number of corals in each size class that were measured in the field for the indicated time interval.

Size class (mm)	Duration of field measurement (months)						Total
	0-3	4-6	7-9	10-12	13-15	16-18	
0-3	-	3	3	1	-	-	7
4-6	1	3	3	5	1	15	28
7-9	-	2	-	-	-	1	3
Total	1	8	6	6	1	16	38

Using the Ford-Walford plot method for parameter estimation, a von Bertalanffy growth curve was also calculated from the CT data (Figs. 12, 13).

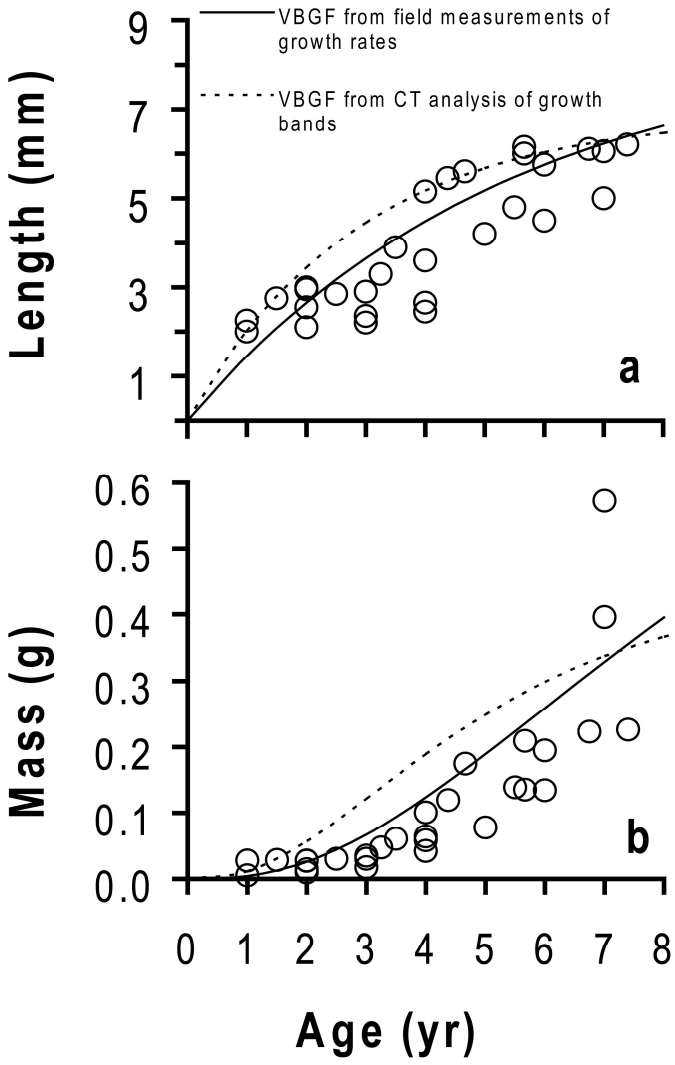

Fig. 12 *Leptopsammia pruvoti*. Age specific von Bertalanffy growth curves (VBGFs) of individuals in Calafuria (Tuscany, Eastern Ligurian Sea), at 16 m depth. The age–size relationship, obtained from application of the von Bertalanffy growth model to linear extension rates measured in the field, is compared to age–size data from CT analysis of skeletal growth bands. (a) Relationship between age and length. (b) Relationship between age and dry skeletal mass. Marked points (circles) are lengths and masses of individuals whose age was determined from CT analyses of growth bands. The age-specific growth model curves for length depicted in (a) were converted in to the mass-growth model curves depicted in (b) by means of the regression $M = 0.001 \cdot L^{2.894}$, where M is dry skeletal mass and L is length, calculated from a previous work on *L. pruvoti* at the same site and depth (Goffredo et al. 2007a).

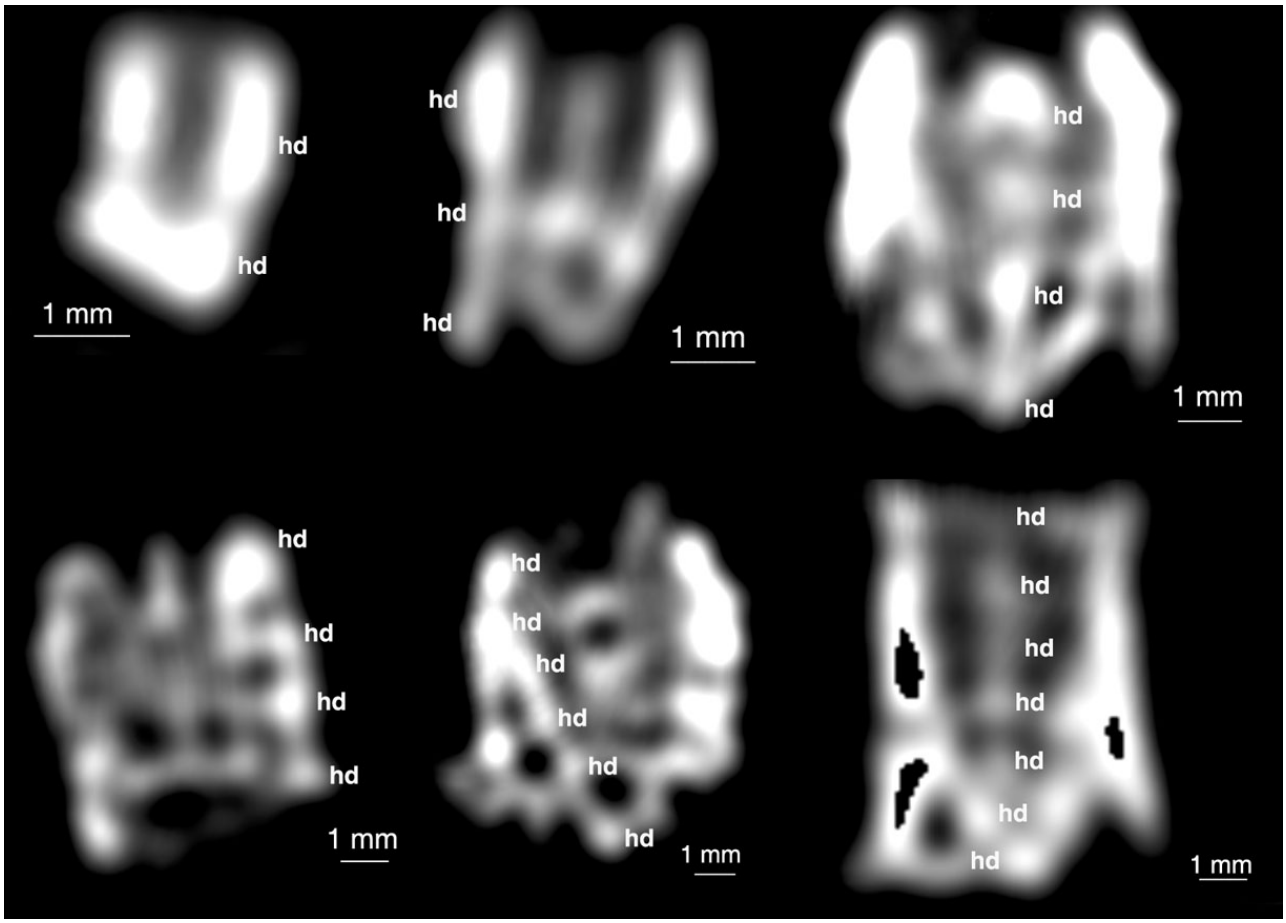

Fig. 13 *Leptopsammia pruvoti*. Computerized tomography (CT) scans of corallites collected in Calafuria at 16 m depth. Sagital CT scan sections are shown (the oral pole is at the top). Each section of annual growth is made up of two bands, a high-density band (*hd*) and a low-density band. Coral age was determined by counting the high-density bands. In these samples, 2-7 high-density bands, corresponding to 2-7 years of growth, are visible. Multiple CT views facilitated the identification of *hd* bands. Slab thickness of each tomography scan was 1 mm.

The linear regression of this plot produced the equation $L_{t+1} = 0.707 \cdot L_t + 2.021$ (r^2 = 0.986; $p <$ 0.01), from which L_∞ = 6.9 mm, K = 0.347. No significant differences were detected between the predicted sizes of the growth curve from field measurements of growth rates and the growth curve from CT analysis of growth bands (Fig. 12). Remarkably similar predictions were generated when comparing the predicted sizes for each age class between the two growth curves [Reliability tests for length-age predictions depicted in Fig. 12a: Cronbach's Alpha coefficient = 0.993; Intraclass Correlation Coefficient = 0.988 (95% CI = 0.924-0.997). Reliability tests for coral mass age based predictions depicted in Fig. 12b: Cronbach's Alpha coefficient = 0.979; Intraclass Correlation Coefficient = 0.953 (95% CI = 0.852-0.986)]. The regressions between observed coral length at known age and predicted length produced overlapping 95% CIs between the two growth curves

(Gulland and Holt growth curve: slope = 0.745-1.490, intercept = -1.754-1.352; Ford-Walford growth curve: slope = 0.500-1.420, intercept = -0.973-2.865). The regressions between observed coral mass at known age and predicted mass produced overlapping 95% CIs between the two growth curves (Gulland and Holt growth curve: slope = 0.534-1.364, intercept = -0.030-0.102; Ford-Walford growth curve: slope = 0.295-1.476, intercept = -0.013-0.174).

Population age structure and survivorship

The size-frequency of individuals observed in the field, when converted to an age-frequency distribution using the above age–size relationship, revealed a young population (Fig. 14a). Within the population sample, 51.0% of individuals were <3 years old (<4 mm in length), i.e. under or at the age of sexual maturity, while few individuals (1.0%) fell into the three oldest age classes: 8, 9 and 10 years. Despite their higher numerical proportion, young individuals contributed only 9.1% of biomass, as shown by the somewhat bell-shaped age-specific yield distribution (Fig. 14b). The observed yield distribution exhibited a peak at 4 years. The largest individuals observed were estimated to be 10 years old (7 mm length). The gradual decrease in number of corals in the older age categories indicates that age structure may be stable (Fig. 14a).

From the above age-frequency distribution, the instantaneous rate of mortality (Z) was estimated using the equation $\ln(N_t) = -0.427 \cdot t + 4.339$ ($r^2 = 0.839$; $p < 0.001$), which produced $Z = 0.427$ and $N_0 = 76.6$. The estimated survival curve for members of this population ($N_t = 76.6 \cdot e^{-0.427t}$ per 128 cm^2 of sampled area) indicated a maximum life span of 13 years (Fig. 14c).

The age-specific curves of growth and survival were used to calculate yield of *L. pruvoti* individuals at Calafuria, in terms of dry skeletal mass per recruit (Fig. 14d). Calculated yield, which was based on the predicted survivorship and age-specific individual biomass, increased rapidly when the individuals were young, due to their rapid increase in size. Yield was maximal at 4-5 years of age (maximum yield = 0.022 g rec^{-1}), after which losses due to mortality overtook gains due to individual growth. The age at maximum yield occurred 2–3 years after the age at sexual maturity (Fig. 14d).

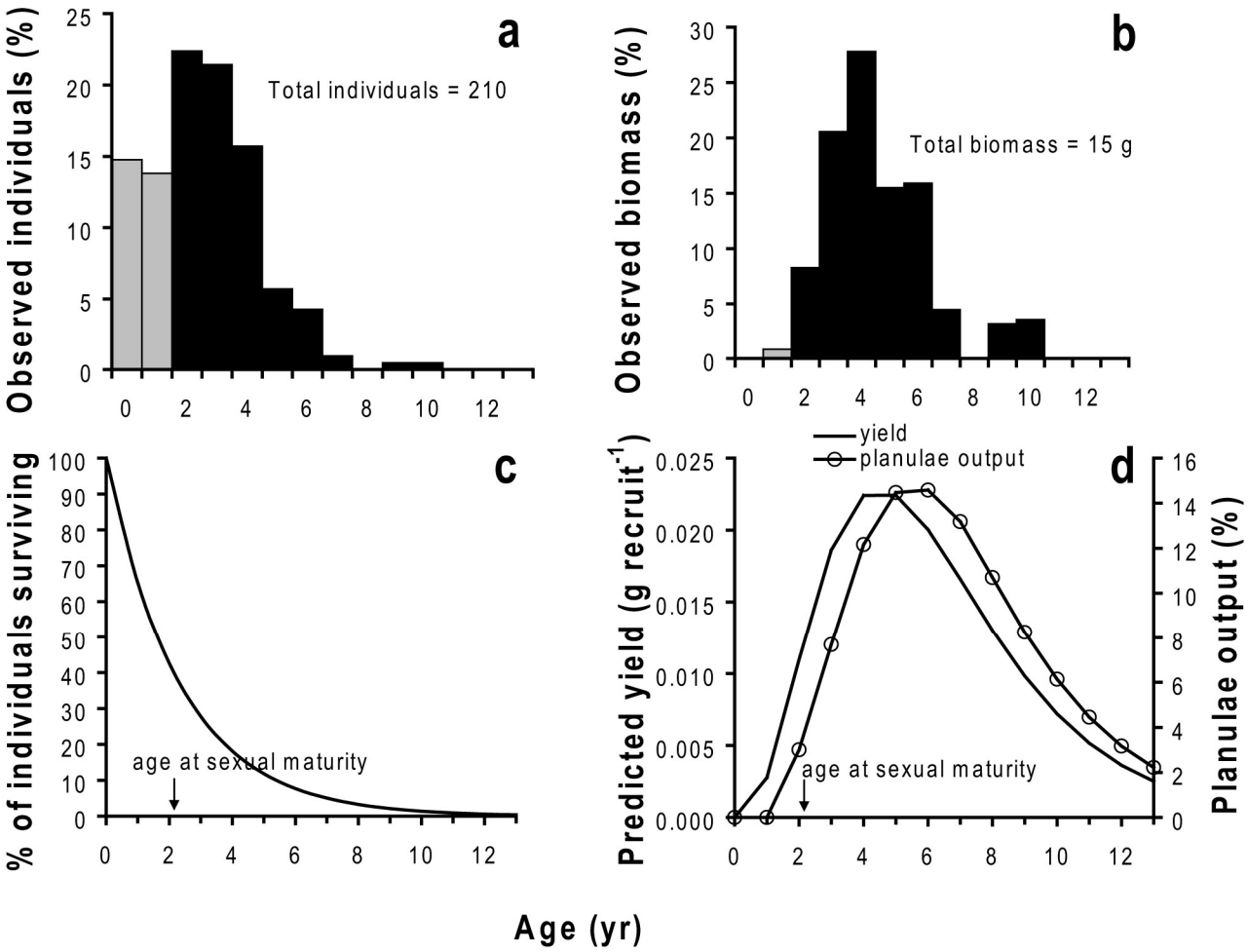

Fig. 14 *Leptopsammia pruvoti.* Age class distribution in terms of number (a) and dry biomass (b) of individuals, survivorship (c), Beverton-Holt population yield curve in dry biomass and reproductive output (d) at Calafuria (eastern Ligurian Sea). Bars for number and biomass of individuals that are shaded grey denote individuals that have not yet reached reproductive size (Goffredo et al. 2006).

Life table

The total number of planulae released during a reproductive season by members of this population was 264,810 larvae m^{-2}. Most reproductive output was by corals 4-8 years of age (Table 7; Fig. 14d). The older classes, though made up of larger polyps having higher fecundity, represented only a small fraction (6.4%) of the reproductive population, and thus contributed a smaller percentage (24.2%) of total population reproductive output (Table 7; Fig. 14c, d). The ratio between estimated reproductive output and recruit abundance estimated in the same area yielded an average "local" larval mortality of 97.7% (95% CI = 84.4-99.6%; Table 7).

Discussion

Growth rate and models

Field measurements of growth rate were highly variable within each size class. Possible sources of this high variation was the different time interval of measurement between corals which can encompass different seasons. While it is reasonable to assume that these corals vary their growth rate throughout the year, the annual average growth rate showed to be a good measure of growth in the sympatric solitary coral *Balanophyllia europaea* (Goffredo et al. 2004a). Using corals measured for only one season may cause problems in species with seasonal differences in growth when normalizing growth rates to a year. However, this bias is limited in this study because only a minor part of the samples was measured for less than one season (Table 8). More data points of growth in the field or longer measurement time could have increased the predictive power of the analysis, but the strong confirmation from CT growth data made more field effort unconvenient. In fact, the growth curve obtained by field measurements was remarkably similar to the one obtained by CT scans, which is based on up to 7 years of growth. This highlights the importance of assessing the growth rate using different independent methods.

Many scleractinian corals grow indeterminately, and thus theoretically have unlimited body size (i.e. even the largest individuals continue to growth; Hughes & Jackson 1985). Unlimited growth is possible through the production of new, energetically self-sufficient modules, and also because energy expendable on growth or reproduction increases proportionally with colony mass (Buddemeier & Kinzie 1976). However, some scleractinian corals reduce their growth rate as they increase in size. Modular scleractinian coral species with size-dependent growth include branching (*Pocillopora* spp.; Grigg & Maragos 1974), massive (*Goniastrea aspera*; Sakai 1998) and free-living colonies (*Manicina areolata*; Johnson 1992). Several cases of size dependent modular growth are also known for octocoral species (Cordes et al. 2001; Bastidas et al. 2004; Goffredo & Lasker 2006). Solitary scleractinian species with size-dependent growth include free-living polyps (many species of mushroom corals; Yamashiro & Nishihira 1998; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003; Knittweis et al. 2009), and attached polyps such as *Leptopsammia pruvoti* (this study), *B. europaea* (Goffredo et al. 2004a), *B. elegans*, and *Paracyathus stearnsii* (Gerrodette 1979). In these species, the determinate growth could be due to a preferential allocation to reproduction of the increased available energy due to larger mass, without investing further energy on somatic growth.

Size profoundly influences the physiological traits, ecological relationships and evolutionary success of organisms (Brown et al. 2000). Within the mechanical constraints of organism design, the environment may strongly affect the ultimate size an individual attains (Sebens 1987). In free-

living corals, which often colonize soft substrata, a genetic limitation on maximum size may represent an adaptation to avoid sinking (Chadwick-Furman & Loya 1992). Among attached organisms, the individuals of some intertidal species tend to be larger in sheltered coves than at wave-exposed sites, which likely reflects the reduced risk of detachment where hydrodynamism is limited (Denny et al. 1985). Alternatively, energetic costs can limit growth. In sea anemones, individuals occupying the lower intertidal grow larger than those inhabiting the upper intertidal, potentially as a result of increased feeding time and decreased aerial exposure (Sebens 1982). Finally, considerable surplus of energy can be apportioned to physiological functions other than growth, such as sedimentation removal, locomotion, and competition, when individuals gradually decrease their calcification rates and have upper size limits (Elahi & Edmunds 2007).

Temperature is strongly linked to coral biometry, physiology, and demography (Harriot & Banks 2002), and may significantly affect the maximum size of individuals in populations (Goffredo et al. 2008). The maximum individual coral length predicted here by the von Bertalanffy model (L_∞ = 6.9-8.6 mm) was similar to that observed in the field population sampled at Calafuria (maximum observed length = 7.3 mm). While 17 mm was once given as the maximum length for *L. pruvoti* individuals (Zibrowius 1980), a positive correlation between annual SST and coral length was recently reported in *L. pruvoti* populations (Goffredo et al. 2007a), with the largest corals (13 mm) reported at Scilla in the Strait of Messina, 625 km south of Calafuria and in warmer waters. A strong positive relationship between annual SST and coral size also occurs in *B. europaea*, another sympatric dendrophylliid coral along the west coast of Italy (Goffredo et al. 2007a).

Population dynamics

In the examined population, the age frequency distribution of individuals > 2 years old showed an exponential decrease in the frequency of individuals with age, with the youngest age classes probably under-represented, which is typical for field samples (Grigg 1984; Babcock 1991; Goffredo & Chadwick-Furman 2003; Goffredo et al. 2004a; Goffredo & Lasker 2008). The under-representation of young corals (0-1 years) was probably a consequence of the difficulty in seeing corals of this size (<3 mm in length). The gradual decrease in the number of corals in the older age categories indicates a population in steady state, in that no age cohorts were missing or over-represented, as would be the case if a major disturbance event had recently altered recruitment patterns (Grigg 1977, 1984; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003; Goffredo et al. 2004a; Santangelo et al. 2007; Goffredo & Lasker 2008). Other examples of coral populations in steady state, with stable age structures, are those of some colonial and solitary stony corals (Grigg 1984; Ross 1984; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman

2003; Goffredo et al. 2004a, 2008), gorgonians (Grigg 1977; Mistri 1995; Goffredo & Lasker 2008), and commercially-important precious corals (Grigg 1984; Santangelo et al. 2004, 2007). In a theoretical population at steady state, the coefficient of correlation of the semi-log regression from which the instantaneous rate of mortality (Z) is estimated has a value r = -1.000 (Pauly 1984). In *L. pruvoti*, this coefficient of correlation was r = -0.916. This value is similar to those calculated for other coral populations reported to occur in a steady state (r = -0.851 to -0.993; Grigg 1984; Ross 1984; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003; Goffredo et al 2004a; Goffredo & Lasker 2008). This indicates that our steady state assumption in order to calculate the instantaneous rate of mortality was not unreasonable. According to population dynamic models, the instantaneous rate of mortality equals the inverse of the mean lifespan of the individuals in a population (turnover time), and hence is equal to their turnover rate, or annual production:biomass ratio (P/B) (Pauly 1984; Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003; Goffredo et al. 2004a). The turnover time for *L. pruvoti* at Calafuria was 2.3 years (calculated as the reciprocal of Z; 95% CI = 1.7-3.6 years). These estimates of mortality rate and maximum life span for *L. pruvoti* appear to be reasonable, in that values derived from the survival curve closely reflect field observations.

Cohort yield of *L. pruvoti* reached its maximum earlier than *B. europaea* at the same locality (age at maximum yield: for *L. pruvoti* 4-5 years, this study; for *B. europaea* 6-7 years, Goffredo et al. 2004a). The age-based cohort yield curve depends on individual rates of mortality and growth. *L. pruvoti* was characterized by higher growth and mortality rates compared to *B. europaea*, both contributing to the early peak of cohort biomass (*L. pruvoti*: K = 0.185-0.347, Z = 0.427, this study; *B. europaea*: K = 0.111-0.126, Z = 0.275; Goffredo et al. 2004a). In other solitary scleractinian corals, the age at maximum cohort yield ranges from 5 years in *Fungia scutaria* to 20 years in *Heliofungia actiniformis* (Chadwick-Furman et al. 2000; Goffredo & Chadwick-Furman 2003; Knittweis et al. 2009).

Life history table

The availability of estimates of population reproductive parameters (Goffredo et al. 2005, 2006) enabled me to construct a static life history table which summarizes the main demographic parameters measured in this population. Most of the population reproductive output came from individuals 4-8 years old (65% of planula production), while the older classes, although composed of larger individuals having higher fecundity, were too infrequent to make a large contribution to reproduction, and therefore accounted only for a small portion of the population overall

reproductive output. On the contrary, in species with decreasing mortality with increasing size, like colonial corals, the largest colonies contribute the most to the reproductive output.

The ratio between larval output and recruit abundance, estimated in the same population, yielded a local larval mortality rate of about 98%, assuming local recruitment. Even though population genetic structure data indicate that local recruitment is likely in *L. pruvoti* (Goffredo et al. 2009), larval migration may affect local mortality. Self recruitment (settlement at the natal site) in marine species has recently been reported to be more frequent than previously suspected, and thus populations may be less open (or more closed) than originally thought (Levin 2006). My estimated local larval mortality for *L. pruvoti* was higher than that reported for the brooding red octocoral *C. rubrum* at the same site (Santangelo et al. 2004), and similar to that reported for the brooding octocorals *M. californica* and *M. fruticosa* in California (Grigg 1977). For marine populations, the number of eggs or larvae required to produce one reproductive offspring that survives the larval and early juvenile stage is poorly known (Botsford et al. 2009). In *L. pruvoti*, accordingly to the life history table, the percent of individuals reaching the age at sexual maturity was 43% (95% CI = 31-58%) and the number of larvae needed for 1 recruit was 44 (95% CI = 6-234), thus 104 larvae (95% CI = 10-754) were required to produce one reproductive offspring.

Life strategies in solitary dendrophylliid corals

The average population abundance of *L. pruvoti* is markedly higher than of other solitary dendrophylliid corals for which population dynamics and reproductive biology have been reported, namely *B. europaea*, endemic to the Mediterranean Sea, and *B. elegans* off North Western America (Table 9). The higher population abundance of *L. pruvoti* is most likely due to localized recruitment of a fraction of the azooxanthellate brooded larvae, which attach to the vault of crevices near the parent polyps, causing a high rate of local inbreeding through mating between close relatives (Goffredo et al. 2009). Even *B. elegans* has a higher population abundance compared to *B. europaea* (Table 9), which is most likely due to the low dispersion ability of the azooxanthellate benthic larvae which attach to the bottom less than 0.5 m from the parent polyp (Gerrodette 1981; Fadlallah & Pearse 1982; Fadlallah 1983). On the other hand, the low population abundance of *B. europaea* may be caused by high dispersion ability of the larvae, which are zooxanthellate, have neutral buoyancy and exhibit swimming and pelagic behavior (Goffredo & Zaccanti 2004; Goffredo et al. 2004a). Symbiotic zooxanthellae contribute to the energy requirements of larvae during dispersion, and may increase their dispersion ability (Richmond 1987; Goffredo & Zaccanti 2004).

Table 9 Life history characteristics of three species of solitary dendrophylliid corals. Most of the data were obtained from previous studies for *Leptopsammia pruvoti* (Goffredo et al. 2005, 2006, 2007a, 2009, and this study), *Balanophyllia europaea* (Goffredo & Telò 1998, Goffredo & Zaccanti 2004, Goffredo et al. 2000, 2002, 2004a), and *B. elegans* (Gerrodette 1979, 1981, Fadlallah & Pearse 1982, Fadlallah 1983, Beauchamp 1993).

	L. pruvoti	*B. europaea*	*B. elegans*
Trophic strategy	Azooxanthellate	Zooxanthellate	Azooxanthellate
Population abundance (mean individuals m^{-2})	10,155	16	563
Rate of demographic renewal			
Maximal coral size (length, mm)	9	21	<10
Turnover time (years)	2.3	3.6	1.3
Maximum longevity (years)	13	20	7
Reproductive biology			
Fecundity	36-105	8-14	2-6
Planula size (mature oocytes / 100 mm^3 polyp)	1,145	2,150	4,000
Period of embryo incubation (months)	1–4	4-5	14-15
Planula size (mean oral-aboral diameter; μm)	1,145	2,150	4,000
Dispersion of planulae	Mix	Pelagic	Benthic
Individual size at sexual maturity [fraction of maximum size (observed size)]	33% (3 mm)	38% (8 mm)	56% (6 mm)
Individual age at sexual maturity [fraction of maximum longevity (actual age)]	15 % (2 years)	20% (4 years)	57% (4 years)

Life history theory predicts that organisms develop different life history strategies to maximize their fitness in environments (Pianka 1970; Stearns 1976, 1989). Thus, organisms have different life history traits as a result of trade-offs among reproduction, growth and survival (Stearns 1989; Roff 1992) under different environmental conditions and selective pressures. Any organism has a finite available amount of energy to partition between growth, maintenance and reproduction (Pianka 1983). Changes in ecological or environmental conditions requiring higher energy for growth or maintenance may thus result in a decreased reproductive output. Concerning reproductive strategies, the classic *r/K*-selection theory (Pianka 1970) has often been used to categorize organisms: *r*-strategists (also called opportunistic species) are characterized by high fecundity, high mortality rates, small body size, small generation time and high dispersion possibility; whereas *K*-strategists usually have the opposite characteristics. Even if the original theory has been reviewed and updated in the last 40 years (Stearns 1976, 1989; Roff 1992), the *r/K* correlates are still widely used to describe life history strategies, and are particularly useful in groups were life history strategies have rarely been studied, like in scleractinians. The usefulness of this method is particularly relevant in dendrophylliid corals, in which the classic *r/K*-selection theory has been used (Table 9). Species that are *r*-strategists are usually dominant in highly disturbed and/or

stressed environments, while *K*-strategists are typically dominant in stable environments. A comparison of the biological characteristics of three dendrophylliid solitary corals (Table 9) reveals that they appear to have evolved mixed strategies. *B. elegans* has demographic renewal with *r*-characteristics and reproduction with *K*-characteristics; *B. europaea* has a *K*-demographic renewal strategy and reproduction with intermediate characteristics; *L. pruvoti* has an *r*-reproductive strategy and demographic renewal with intermediate characteristics. However, this comparison should be taken with caution, since life histories of the above compared species have been studied only in one site, and differences may exist between populations subject to different environmental conditions or selective pressures.

Conclusion

This is the first field investigation of the relationships between environmental parameters and growth and demography of a Mediterranean coral, and highlights risks of losing Mediterranean marine biodiversity over the next decades.

Overall, the growth and demographic parameters of the two studied species resulted negatively affected by rising sea surface temperature. This was particularly evident on the symbiotic species, *Balanophyllia europaea*, whose skeletal density, calcification, population abundance and stability, and presence of young individuals in the population all correlated negatively with temperature. Analogue analyses on the azooxanthellate *Leptopsammia pruvoti* are currently underway, however, also in this species the skeletal density correlated negatively with temperature, even if the decrease was less marked than in *B. europaea*. This led me to hypothesize that rising temperature could strongly repress the photosynthesis of *B. europaea* symbionts, with a consequent negative influence on the calcification process and on the energy available to the polyp for all its physiological processes. The weaker negative effects on *L. pruvoti* could depend on a negative effect of rising temperature on the process of calcification itself, but, in this case, without the superimposed inhibition on photosynthesis. Analyses of the photosynthetic efficiency on *B. europaea* specimens maintained in aquaria at different temperatures are currently underway, and preliminary results seem to support my hypothesis.

The investigations on the relationships between environmental parameters and population dynamics of these two species and other Mediterranean corals will continue in the next 5 years within the project "Corals and Global Warming: The Mediterranean versus the Red Sea" (CoralWarm; www.coralwarm.eu), which was recently funded by the European Research Council within the "IDEAS Advanced Grant" scheme of the 7th Framework Program of the European Union. This project will investigate the effects of rising temperature and acidification on coral key species from the Mediterranean and Red Sea, considering all aspects of growth, population dynamics, reproduction, physiology, skeletal mechanical and structural properties and gene expression.

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